ENVIRONMENTAL AND ECOLOGICAL IMPLICATIONS OF LARGE MAMMALS FROM UPPER PLEISTOCENE AND HOLOCENE SITES IN SOUTHERN AFRICA

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(With 5 figures, 7 tables and 1 appendix)

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ABSTRACT

There are now more than seventy-five Upper Pleistocene and Holocene localities in southern Africa that have provided analysable remains of large mammals. The purpose of this paper is to summarize the information these remains have provided on past environments, on the evolution of man–environment relationships, and on the ecology and demise of extinct species.

For the purposes of discussion, the fossiliferous Upper Pleistocene and Holocene sites are divided among six modern southern African ecozones, distinguished from one another on climatic, phytogeographic, and zoogeographic grounds. Changes in large mammal distributions or in species frequencies that probably reflect Upper Pleistocene and Holocene environmental change can be demonstrated in all six ecozones, but a well-defined pattern of change in mammalian faunas that can be correlated with a pattern of long-term environmental change established on other grounds can be demonstrated in only one ecozone. This is the Cape Zone, where cooler intervals during the Upper Pleistocene repeatedly witnessed an increase in grazing ungulates relative to browsers. In part, the failure of comparable patterns to emerge in other zones may reflect the fact that Upper Pleistocene environmental and faunal change was greater in the Cape Zone than elsewhere, but in large part it almost certainly reflects the better overall quality of data from the Cape—more well-dated sites and more relatively large faunal assemblages for which detailed numerical data are available.

The greater quantity and higher quality of data from the Cape also make it the only ecozone in which there is a substantive basis to discuss: (i) long-term changes in human ability to obtain large mammals; and (ii) the reasons for the disappearance of several large mammal species which were common in various parts of southern Africa during the Upper Pleistocene. The Cape data suggest: (i) that Middle Stone Age people were less proficient hunter–gatherers than their Later Stone Age successors; and (ii) that a combination of environmental change and the greater hunting proficiency of Later Stone Age peoples was responsible for the large mammal extinctions.

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AIMS AND BASIC DEFINITIONS

As a result of research undertaken mainly in the 1960s and 1970s, there are now more than seventy-five Upper Pleistocene and Holocene localities in southern Africa that have provided analysable remains of large mammals. This paper aims to summarize the information these remains have provided on past environments, on the evolution of man–environment relationships, and on the ecology and demise of extinct species.

For the purposes of this paper, southern Africa is defined relatively broadly to include the Zambesian, Transvaalian, Kalaharian, Basutolian, Karoo–Namaqualian, and Cape Ecozones of Devred, as presented in De Vos (1975) (Fig. 1 here). The ecozones themselves are defined on the basis of climatic, phytogeographic, and zoogeographic features which are summarized below (based mainly on information in De Vos (1975) and Brown (1965)). The zones are of course abstractions in the sense that they grade into one another rather than being sharply bounded, and within each there is important climatic, phytogeographic, and zoogeographic variation, as determined for example by great differences in altitude, subsurface drainage, or proximity to permanent water. However, the zones clearly reflect gross differences in the historic distribution and relative abundance of large mammal species and therefore have definite value as a first basis for gauging the palaeoenvironmental significance of fossil mammal faunas.

In modern political terms, southern Africa, as defined here, comprises especially the countries of Angola, Zambia, Malawi, Mozambique, Zimbabwe Rhodesia, Botswana, South West Africa (Namibia), South Africa, Lesotho, and Swaziland. The approximate locations of the principal fossiliferous Upper Pleistocene and Holocene sites within these countries are shown in Figure 2, from which it is clear that the overwhelming majority are located in South Africa, South West Africa, Zimbabwe Rhodesia, and Zambia. In general, blank spots on the map reflect the absence of interested researchers as much or more than any other factor. Undoubtedly, many pertinent sites especially wait to be discovered or excavated in Angola, Botswana, Mozambique, and Malawi.

For the purposes of this paper, the Upper Pleistocene and Holocene have been taken to comprise the time interval represented by stages 1 through 5 of the

Fig. 1. Southern African ecozones, with the most prominent suid, bovid, and equid species found in each. The outlines and names of the zones are from De Vos (1975). Information on species distributions was obtained primarily from Ansell (1971*a*, 1971*b*), Ellerman *et al.* (1953), Joubert & Mostert (1975), Smithers (1966, 1971), and Smithers & Lobão Tello (1976).

deep-sea core oxygen-isotope stratigraphy, that is, approximately the last 130 000 years. These stages are listed in Table 1, along with the temperature conditions they are believed to reflect and their dates, in so far as these have been established. In conventional terms, stage 1 may be equated with the Holocene, stages 2–4 with the 'Last Glacial', and stage 5 with the 'Last Interglacial', though some authorities would prefer to restrict the Last Interglacial to substage 5e, the only part of stage 5 that compared in overall warmth with the Holocene. In so far as it is possible below, the oxygen-isotope stage numbers are used in preference to the terms 'Last Interglacial' and 'Last Glacial', since the stages more fully reflect the true complexity of Upper Pleistocene and Holocene climatic change, particularly in the latitudes of southern Africa (roughly 10°S to 35°S).

'Large mammal' has been defined very loosely to include all mammalian species in which adults weigh at least 0,7–0,9 kg. The principal creatures excluded by this definition are bats, insectivores (except hedgehogs), and rodents (except primarily springhare, cane rats, the largest of the mole rats, and, of course, porcupines). The rationale for excluding 'small mammals' is that this paper is mainly concerned with mammalian remains as reflections of past human ecology, and it seems unlikely that people have ever systematically exploited mammals weighing less than 0,7–0,9 kg. Circumstantially, this proposition is supported by the fact that where small mammal remains have been found in large quantities in southern African sites (for example, at Redcliff Cave, Wonderwerk Cave, Die Kelders Cave 1, Byneskranskop Cave 1, Boomplaas Cave A, and Nelson Bay Cave), they are clearly concentrated in layers where artefacts and bones of large mammals are rare. This suggests that the small mammals were

TABLE 1

Upper Pleistocene oxygen-isotope stages defined in deep-sea cores (based mainly on Shackleton & Opdyke (1973, 1976)).

Approximate years B.P.	*Oxygen-isotope stage*	*Inferred world climate*
0		
	1	very warm
12 000		
	2	very cold
32 000		
	3	cold with warmer oscillations
64 000		
	4	very cold
75 000		
	5a	warm
92 000	5b	cold
	5c	warm
109 000	5d	cold
	5e	very warm
128 000		–

brought in mainly by predatory birds who occupied the sites when people were absent.

Of course, even though (or in part because) small mammal remains are generally not a product of human activity, they constitute a potentially valuable source of information about past environments, and their value in this regard is enhanced by the fact that it is often possible to obtain very large samples from relatively small excavations. Pertinent examples of palaeoenvironmentally oriented small mammal studies in southern Africa are those of Brain (1974*a*; Brain & Brain 1977) in the Namib Desert, and of Avery (1977 and in prep.) in the southern Cape Province. Brain has pointed out that fluctuations in the abundance of the principal species represented in the relatively simple microfaunas of the Namib can be used to monitor past changes in the amount of grass cover and of sand v. gravel in the vicinity of a site. In the more complex situation of the southern Cape, with a wider variety of well-represented microfaunal species, Avery is using sophisticated statistical procedures to detect relatively subtle changes in microfaunal communities, with the goal of checking and amplifying inferences on Upper Pleistocene and Holocene environmental change drawn from parallel studies of large mammal bones, palaeobotanical remains, and sediments.

MATERIALS AND PROBLEMS

The basic materials on which this paper is based are lists of large mammal species reported from Upper Pleistocene and Holocene sites in southern Africa. Both archaeological and non-archaeological sites have been surveyed, but among the archaeological ones, the focus is almost exclusively on sites occupied by Stone Age (v. Iron Age) people. People making stone artefacts were the only human occupants of southern Africa during the Pleistocene and most of the Holocene, and they persisted into the historic period over much of the subcontinent, especially in the Cape, Karoo–Namaqualian, and large parts of the Basutolian and Kalaharian Ecozones.

In the Zambesian and Transvaalian Zones, Stone Age people were progressively displaced by Iron Age agriculturists, beginning in the first centuries A.D. The Iron Age people were immigrants from further north, who subsequently also penetrated into those parts of the Basutolian and Kalaharian regions where their system of mixed farming was practicable. Iron Age faunas have been analysed from sites in Zambia by Fagan (1967; also Fagan *et al.* 1969), in Malawi by Voigt (1970, 1973, 1977), in Rhodesia by Brain (1974*b*) and Huffman (1974, 1975), in Botswana by Welbourne (1975), in the Transvaal by Voigt (1978) and Welbourne (1971, 1973), in Natal by Klein (as reported in Maggs & Michael 1976), and in the Orange Free State by Maggs (1975), but for the purposes of this paper the utility of the samples is limited, because most of them are small and they tend to be dominated by introduced domesticates (cattle, sheep and/or goats). However, the Iron Age lists have been scanned carefully for evidence they may contain on the distribution of indigenous mammals in relatively recent

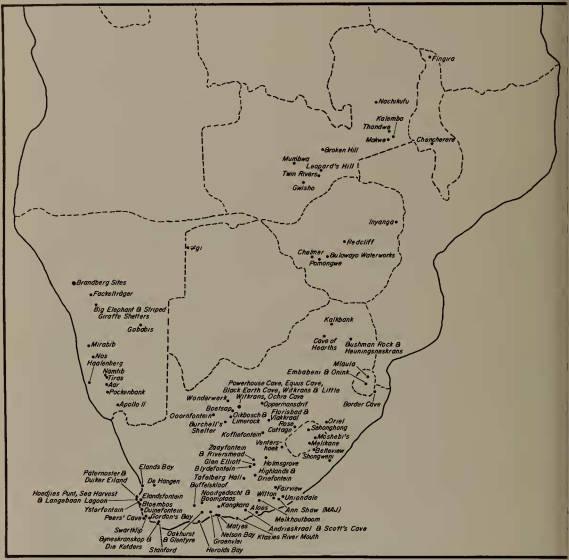


Fig. 2. Approximate locations of the Upper Pleistocene and Holocene fossiliferous sites mentioned in the text.

times. For the most part, the lists support the distributional information that can be gleaned from early European travellers' reports or more recent historical sources, the most important exception being the presence of a possible gazelle in Malawi (Voigt 1973) and Natal (Klein unpub. in regard to the bovid listed as '*incertae sedis*' in Maggs & Michael 1976).

The non-archaeological and Stone Age sites which have provided the faunal lists on which this paper is based are listed in Tables 2–7. Since there are many sites and many of them are multilevel, it was not practical to reproduce the actual faunal lists here, but the overwhelming majority of them have been or soon will be published in sources listed in the tables.

In analysing the lists for palaeoenvironmental and palaeoecological information, the writer encountered two basic kinds of problems—ones that involved dating and ones that involved sample size and description. With regard to dating, the writer's major goal in most instances was to correlate a fauna with the appropriate oxygen-isotope stage as an important prerequisite to gauging its palaeoenvironmental implications. The isotope stage assignments on which the writer settled are presented in Tables 2–7, but even a rapid reading of the tables will show that in many instances no precise stage assignment was possible. The most secure stage (or substage) assignments are based on radiocarbon dates or on dates inferred from associated artefact assemblages whose radiocarbon ages are fairly well established. In particular, even where accompanying radiocarbon determinations were absent, the writer assumed that any southern African artefact assemblage that contained potsherds postdates 2 000 B.P. (that is, belongs to 'isotope stage 1, late'), that all assemblages which are readily assignable to the Wilton Industrial Complex of the Later Stone Age postdate 10 000 B.P. (belong to isotope stage 1), and that all assemblages which are classically Middle Stone Age antedate 30 000 B.P. (antedate isotope stage 2).

The principal dating difficulty stems from limitations inherent in the radiocarbon method, at least as practised by most laboratories, which make it relatively unreliable for dating sites that are older than 25 000 years, and of little or no utility for the precise placement of sites that are older than 40 000 years. For the moment, the most practical method of placing sites more precisely within the interval between 25 000–40 000 and 130 000 years is to correlate the sequence of climatic events they sometimes record with the general sequence of Upper Pleistocene climatic stages presented in Table 1. There are many sites to which such a dating procedure may never be applicable, and it has so far been applied only to a handful (especially to Border Cave (Butzer, Beaumont & Vogel 1978), Klasies River Mouth (Butzer 1978*a*), and various Cape coastal sites stratified in long aeolianite sequences (Butzer pers. comm.)). As a result, most southern African sites that are of earlier Upper Pleistocene age cannot at present be dated more precisely, even relative to one another, and this is a major obstacle to reconstructing patterns of environmental and cultural change. It is even possible that some supposedly earlier Upper Pleistocene localities actually date from the later part of the Middle Pleistocene (before 130 000 years ago), an interval of time within which more precise dating is also extremely difficult. Neither artefacts nor fauna are very helpful in this context, since sites which have been dated on geological grounds to the late mid-Pleistocene (especially the lower levels of Border Cave (Butzer, Beaumont & Vogel 1978), the principal faunal occurrence at the Florisbad spring site (Butzer, Beaumont & Vogel 1978; Butzer pers. comm.), and Duinefontein 2 (Butzer, Beaumont & Vogel 1978; Butzer pers. comm.) contain artefact and/or faunal assemblages which are not easy to distinguish from those found at undoubted earlier Upper Pleistocene localities.

The problems with sample size and description are as serious as those with dating, though they are perhaps more easily avoidable in future research, since they generally stem from obvious deficiencies in excavation and analysis. The principal difficulty is that for many faunas, particularly those excavated prior to 1950, species lists have often been presented with little or no indication of absolute or relative species abundance, and, even where such indications are available, their utility is often vitiated by the fact that overall sample size is either not presented or is clearly very small. The absence of species frequency estimates and/or small sample size make it difficult, if not impossible, to determine in most instances if the differences between one faunal sample and another could be due simply to chance or if the differences are more likely to reflect differences in palaeoenvironments or in the agencies that accumulated the samples. It was, of course, to establish differences in palaeoenvironment or in agency of accumulation that the writer examined the faunal lists in the first place.

A further problem is that even where indices of species abundance have been presented and sample sizes are reasonable, the indices are not always strictly comparable. Because of limited experience, a lack of adequate comparative materials, or a shortage of time, some analysts have confined their identifications and counts only to the most diagnostic bones (usually teeth), while others have identified and counted a much wider range of skeletal parts. Further, in estimating species abundance, some investigators have presented the numbers of identifiable bones by which each species in a fauna is represented, while others have calculated the minimum numbers of individuals from which the bones are derived.

Even minimum individual counts are not necessarily comparable among sites because of differences in the kinds of provenience units to which counts have been attached or possible differences in the way in which the counts were calculated. At many sites, the provenience units are arbitrary spits that do not necessarily represent discrete occupations, and the minimum individual counts for any spit may well include individual animals that are also represented by bones in adjacent spits. In such a case, the counts may well be 'biased' versus counts from another site where the provenience units are natural layers that represent discrete occupations in which bones from the same individuals are very unlikely to occur. As an example of how methods of calculation may affect minimum individual counts, some investigators sort paired elements into lefts and rights and take the minimum number of individuals represented by the element to be the higher number, left or right. Others simply divide the total number for the element by two. This and other differences in method of calculation are particularly likely to affect results in samples that are relatively small, as most southern African ones are.

Problems of sample size and description are more acute for sites in some areas than in others, and the best, most complete information, expressed in terms that make it possible to compare samples fairly rigorously, is available for the Cape Ecozone. The Cape Zone is also relatively rich in sites that are reasonably well dated, including several that sample the same time intervals, so that inferences about environmental or cultural change may be based on patterns which have been established at several localities. In other ecozones, the overall quality of the data is generally less satisfactory, and the palaeoenvironmental and palaeoecological inferences they allow are consequently more limited.

MAMMALIAN EVIDENCE FOR ENVIRONMENTAL CHANGE

In most cases, it is impossible to assume that the relative abundance of the mammalian species in a fossil assemblage reflects their relative abundance in the live community from which they were derived. By and large, it is far more reasonable to assume that their relative frequencies were altered in the process of bone accumulation (site formation), and generally speaking, the extent of alteration is impossible to determine. This makes it difficult to use most fossil faunas for the detailed reconstruction of an environment at any particular point in time.

On the other hand, there are instances of faunal samples that were accumulated by essentially the same agency (for example, Middle Stone Age people), whose effect in altering or 'biasing' species frequencies was probably more or less the same for all the samples. Differences in species frequencies between samples are then most likely to reflect a difference between the palaeoenvironments from which the samples were derived, and the nature of the environmental difference may be reasonably clear, even if the exact nature of the separate environments is not. More concretely, it may be possible to say, for example, that one environment contained more grazing animals than another, even if it is not possible to say precisely how many grazers were present in either environment.

And even if species frequencies in fossil faunas are not directly comparable to ones in living faunas, sometimes fossil faunas contain species which were never observed in the region of a site and which seem inappropriate to the region, given the known habitat preferences of the species elsewhere. In such instances, the mere presence of a species may be indicative of past environmental difference or change.

The purpose in this section is to present and interpret the available evidence for environmental change during the Upper Pleistocene and Holocene of southern Africa, as it is reflected in former large mammal distributions and in changes through time in large mammal species frequencies. In so far as it is possible, an attempt has also been made here to determine the extent of congruency between environmental change reflected in large mammal faunas and change that has been established from other lines of evidence or that was perhaps predictable, given the placement of faunas in different global climatic (oxygen-isotope) stages.

The discussion will proceed ecozone by ecozone, starting with the most northern and ending with the most southern. For obvious reasons, the opening descriptions of the ecozones will emphasize the larger mammals they contain, particularly the species of bovids, equids, and suids. These species are the most common large mammals in the fossil faunas and also the ones whose past distributions or frequencies seem to have altered most dramatically. Least useful from a palaeoenvironmental point of view are the carnivores, both because they tend to be relatively rare in the fossil faunas and because most species, particularly the larger ones, are much less tied to particular habitats than the herbivores they prey on. They are therefore palaeoenvironmentally much less informative.

THE ZAMBESIAN ECOZONE

The Zambesian Zone is approximately coincident with the 'miombo woodlands', a vast stretch of wooded grassland extending more than 2 500 km from west to east and 1 200–2 000 km from north to south. In modern political terms, the Zambesian Zone comprises southern Tanzania, southern Zaïre, most of Angola, Zambia, Malawi, northern Mozambique, and northern Zimbabwe Rhodesia.

Rainfall throughout the Zambesian region averages more than 500 mm/a, but it is almost entirely restricted to the summer months (December to May). On relatively well-drained ridges, hills, or interfluves, the vegetation tends to consist of tall grass interspersed with deciduous trees (especially *Brachystegia* and *Julbernardia*) that lose their leaves in the dry season. In river valleys and along drainage lines (called dambos), trees, consisting mainly of acacias, are less common, and tall grasses predominate. Along the margins of river valleys, and especially in the southernmost part of the Zambesian Zone, the predominant tree in the savanna tends to be mopane (*Colophospermum mopane*). In typical miombo woodland (dominated by *Brachystegia* and *Julbernardia*), the grasses are of the 'sour' type that lose most of their nutritive value in the dry season. However, in mopane woodland, 'sweet' grasses that maintain their palatability throughout the year are more common, and as a consequence, mopane country tends to maintain a higher biomass of large grazing animals. It is only on the floodplains of the large rivers, however, that the Zambesian Zone supports numbers of large grazers to rival the numbers that occur or occurred on east and South African grasslands (in the Eastern and Basutolian regions of Figure 1).

Although the number of large mammals per unit area was generally less in the Zambesian Zone than in some others, the opportunities that it offers both browsers and grazers have led to unrivalled species diversity. In terms of biomass, browsers were probably secondary overall, but at least locally, bushpig, bushbuck, Sharpe's grysbok, greater kudu, and grey duiker were (and in places still are) numerous in areas where browse and good cover are readily available. The principal grazers were Burchell's zebra, Lichtenstein's hartebeest, tsessebe, blue wildebeest, and warthog, occurring both in open woodland and in more open dambo areas. They shared the open woodland with sable antelope, roan antelope, and impala, which also tended to frequent more closed woodland. Southern reedbuck, waterbuck, puku, sitatunga, and especially lechwe and buffalo occurred on floodplains or floodplain margins. Eland, giraffe, elephant, and black rhinoceros occurred more or less throughout. White rhinoceros were locally common, and hippopotamus were present in all the large rivers. Among the smaller mammals, vervet monkey, baboon, hyraxes, hares, porcupine, cane rat, and springhare were all common, as were a wide range of carnivores, including all the top predators found elsewhere in Africa.

The pattern of Upper Pleistocene and Holocene environmental change in the Zambesian Zone is far from being established. The best available palynological and geomorphic data probably come from the Lunda area of north-eastern Angola (Clark 1963) and Kalambo Falls in north-eastern Zambia (Clark 1969) (also summaries of both areas in Butzer 1971*a*: 341–345). It is now clear that major parts of both sequences which were formerly assigned to the earlier Upper Pleistocene in fact date from the Middle Pleistocene, and also that there are problems with the precise chronological placement of parts of the sequences which are Upper Pleistocene in age. But the Lunda and Kalambo data still show that the later Pleistocene locally witnessed a succession of cooler and warmer phases, as well as a succession of wetter and drier ones. During the cooler periods, average yearly temperatures may have been as much as 3–5°C below what they are today. The major cool episodes probably correspond to the world-wide periods of colder climate reflected in deep-sea cores, but there was not necessarily correspondence between cooler periods and wetter ones. In fact, it is even possible that as it became wetter in one part of the Zambesian Zone, it became drier in another. It is now clear that Upper Pleistocene and Holocene periods of greater precipitation to the south-west of the Zambesian Zone (in the Kalaharian one) were often contemporaneous with drier ones to the north-east (in the Eastern one) (Butzer 1978*b*), and the situation in various parts of the Zambesian Zone must be investigated empirically before any generalizations may be made.

The Upper Pleistocene and Holocene sites in the Zambesian Zone that have provided remains of large mammals are listed in Table 2, along with the probable or suggested correlation of the sites (or of levels within them) with various oxygen-isotope stages. It is clear that faunal remains are available from sites correlated with several different stages, though precise stage placement is problematic in several instances (see Table 2 and below).

As a group, regardless of age, isotopic stage placement, or cultural associations, the various Zambesian sites tend to be dominated by large grazing

TABLE 2

Upper Pleistocene and Holocene sites that have provided remains of large mammals in the Zambesian Ecozone.

SITE	GENERAL SOURCE	PERSON IDENTIFYING FAUNA AND SEPARATE PUBLICATION, IF ANY	ARCHAEOLOGICAL ASSOCIATIONS
Isotope Stage 1, late (c. 5 000–0 B.P.)			
Fingira Rock Shelter	Sandelowsky & Robinson (1968)	J. E. Mawby	LSA
Chencherere Rock Shelter II	Clark (1973)	D. Crader (n.d.)	LSA
Thandwe Rock Shelter	Phillipson (1976)	J. Harris	LSA
Kalemba Rock Shelter (levels O–S)	Phillipson (1976)	J. Harris	LSA
Makwe Rock Shelter	Phillipson (1976)	B. M. Fagan & D. Davis	LSA, Iron Age
Leopard's Hill Cave (spits 1–8)	Miller (1969, 1971)	R. G. Klein	LSA
Gwisho Hot Springs B, C	Fagan & Van Noten (1971)	B. M. Fagan	LSA
Gwisho Hot Springs A	Gabel (1965)	L. H. Wells	LSA
Isotope Stage 1, early (c. 12 000–5 000 B.P.)			
Leopard's Hill Cave (spits 9–16)	Miller (1969, 1971)	R. G. Klein	LSA
Isotope Stage 1, undifferentiated (c. 12 000–0 B.P.)			
Nachikufu Cave	Clark (1950); Miller (1969, 1971)	H. B. S. Cooke (1950)	LSA
Mumbwa Caves (LSA levels)	Clark (1942)	R. Broom; H. B. S. Cooke (1950)	LSA
Inyanga (LSA caves)	Summers (1958)	H. B. S. Cooke (1958)	LSA
Isotope Stage 2 (c. 32 000–12 000 B.P.)			
Kalemba Rock Shelter (levels L–N)	Phillipson (1976)	J. Harris	LSA
Leopard's Hill Cave (spits 17–40)	Miller (1969, 1971)	R. G. Klein	LSA
Redcliff Cave ('Tshangula' levels)	Brain (1969*a*); Brain & Cooke (1967); C. K. Cooke (1978)	R. G. Klein (1978*a*)	LSA
Isotope Stage 3 (c. 60 000–32 000 B.P.)			
Redcliff Cave ('Later Bambata' levels)	Brain (1969*a*); Brain & Cooke (1967); C. K. Cooke (1978)	R. G. Klein (1978*a*)	MSA
Isotope Stage 4 (c. 75 000–64 000 B.P.)			
Redcliff Cave ('Earlier Bambata' levels)	Brain (1969*a*); Brain & Cooke (1967); C. K. Cooke (1978)	R. G. Klein (1978*a*)	MSA
Isotope Stages 3, 4 and/or 5, undifferentiated	*(c. 128 000–32 000 B.P.)*		
Kalemba Rock Shelter (levels G–K)	Phillipson (1976)	J. Harris	MSA
Broken Hill (in part)	Clark *et al.* (1950)	Hopwood (1928); H. B. S. Cooke (1950); Leakey (1959)	MSA
Mumbwa Caves (MSA levels)	Clark (1942)	H. B. S. Cooke (1950)	MSA
Twin Rivers Kopje	Clark (1971)	H. B. S. Cooke	MSA

ungulates, particularly Burchell's zebra, warthog, and alcelaphine antelopes (blue wildebeest, hartebeest, and bastard hartebeest). These are the creatures which were predominant in most parts of the Zambesian Zone historically, suggesting definite limits to overall Pleistocene and Holocene environmental change, particularly as compared to the Cape Zone (discussed below) in which historically abundant mammals disappeared or became very rare on several occasions during the same interval.

Where there is deviation from the general pattern of dominance by zebra, warthog, and alcelaphines, it is toward an emphasis on other large grazing ungulates whose local abundance was predictable from the location and dating of a site. Thus, lechwe and buffalo are especially well represented at the late mid-Holocene ('isotope stage 1, late') spring sites at Gwisho, located on the margin of the Kafue floodplain on which these creatures were quite common historically (large herds of lechwe still occur near by). Zebra, warthog, blue wildebeest, and impala are also well represented in the Gwisho sites, presumably reflecting their prominence in the typical miombo woodland that flanks the Kafue floodplain at Gwisho. The long-term persistence of adjoining Kafue floodplain and miombo woodland habitats is clearly suggested by the much earlier (Middle Stone Age) fauna from Twin Rivers Kopje, which, like the Gwisho sites, is located on the margin of the Kafue floodplain, and which has also provided a fauna in which lechwe, wildebeest, and zebra are abundant, although precise numerical estimates are not available.

A further site in which creatures favouring near-water situations are very common is Kalemba Rock Shelter which has provided a relatively large number of bushpig and waterbuck remains. It is not clear that these creatures (at least waterbuck) were so abundant near Kalemba historically, and since their remains come principally from layers that probably belong in isotope stage 3 or 4, they may reflect once moister conditions near by.

The best evidence for environmental change in the Zambesian Zone, as reflected in mammalian fauna, comes from Redcliff Cave, where three species are present which did not occur in the Zambesian region in historic times, and which are so far unknown in any fauna clearly postdating isotope stage 2. These species are the blesbok, the common springbok, and the mountain reedbuck.

In an earlier publication on the Redcliff fauna, the writer suggested that the 'Tshangula' industry at the site was a late Middle Stone Age manifestation, similar perhaps to the Howieson's Poort variant of the Middle Stone Age further south (Klein 1978*a*). However, with the appearance now of a more complete report on the artefacts (C. K. Cooke 1978), the writer believes the 'Tshangula' industry is more likely to be an early Later Stone Age variant, dating to between 30 000 and 20 000 years B.P., as is in fact suggested by the single available radiocarbon date. This would place the 'Tshangula' industry and associated fauna in isotope stage 2.

The underlying Bambata levels, which are undoubtedly Middle Stone Age, are clearly beyond the range of radiocarbon dating, and their placement in one or another isotope stage is not straightforward. However, Brain's (1969*a*) analysis of the Redcliff sediments is helpful in this regard. This shows that $CaCO_3$ concentration is relatively low and the matrix is relatively coarse in the earlier Bambata and especially in the Tshangula levels, perhaps reflecting stronger water flushing of the deposits, in turn reflecting moister climate. During accumulation of the intervening later Bambata levels, with a higher $CaCO_3$ content and finer matrix, conditions may have been generally drier.

If the Tshangula horizons are properly placed in isotope stage 2 and this was a relatively moist time near Redcliff, it seems most reasonable to place the earlier Bambata horizons, indicating comparable moistness, in the next oldest isotope stage that was generally comparable to '2' world-wide. This would be '4' (= early 'Last Glacial'). The intervening later Bambata levels, with their sedimentologic evidence for relative dryness, would then date from stage 3, during which world climates were generally less different from present ones than during stages 2 and 4. It is interesting in this context that the three 'exotic' species found at Redcliff are significantly more common in the Tshangula and earlier Bambata levels than in the later Bambata ones, suggesting that these species were locally most abundant during relatively moist intervals. All three presumably extended their ranges to Redcliff from regions much further south where they were common historically. Range extension Equatorwards (presumably as a result of vegetational change) might itself be taken as evidence for cooler conditions, moister conditions, or both.

The presence of common springbok in the Zambesian Zone is confirmed for stage 2 at Leopard's Hill Cave, where both radiocarbon dates and well-described associated (early Later Stone Age) artefacts leave no doubt about stage placement, although the overall Leopard's Hill faunal sample is too small for detailed palaeoenvironmental interpretation. There is no evidence that springbok survived into stage 1 (the Holocene) in the Zambesian region, but during this interval, a close east African relative of the springbok, the Thomson's gazelle, apparently penetrated the Zambesian Zone at least as far south as Kalemba Rock Shelter and perhaps also into Malawi, where a possible gazelle has been recorded in Iron Age sites (Voigt 1973) and in the broadly contemporaneous Later Stone Age deposits of Chencherere Rock Shelter II (Crader n.d.). In fact, the 'tommie' may have extended through the eastern portion of the Zambesian Zone into the Transvaalian one, if the writer's tentative identification of material from the Iron Age site of Ntshekane in the Tugela Basin of Natal is correct (Maggs & Michael 1976). Why the species did not occur in the Zambesian and Transvaalian Zones historically is not clear, but perhaps its absence is related in some way to the introduction and proliferation of domestic stock in Iron Age times.

THE TRANSVAALIAN ECOZONE

On the southern margin of the Zambesian Zone, mopane woodland tends to give way to shrubby acacia steppe or bushveld in a semi-arid setting. This semi-arid country, running more or less across the continent, constitutes the Transvaalian Ecozone. As in the Zambesian Zone, rainfall is restricted almost entirely to summer, but the average is generally less than 500 mm/a, and there are great differences in total amount from year to year.

Of all the ecozones considered here, the Transvaalian one is the least satisfactory as a unit. It might well be better to consider it as three zones: (i) a western one, comprising the northern Transvaal, southern Zimbabwe Rhodesia, northern Botswana, northern South West Africa, and southern Angola; (ii) an eastern one, comprising the eastern Transvaal, adjacent south-western Mozambique, and eastern Swaziland; and (iii) a narrow southern extension comprising the Natal and south-eastern Cape coastal strips and their immediate hinterlands as far south-west as Port Elizabeth.

The western portion of the Transvaalian Zone, from the northern Transvaal westwards, is the driest part. The vegetation is typically grassland with interspersed shrubby trees, among which acacias are often most prominent. In a sense, the area is not so much a distinct ecozone as a transitional region between the Zambesian Zone to the north and the Kalaharian one to the south. Grazers (including blue wildebeest, Cape hartebeest, tsessebe, Cape buffalo, springbok, gemsbok, Burchell's zebra, and warthog) are most common, but browsers (greater kudu, bushbuck, giraffe, black rhinoceros *et al.*) and mixed feeders (eland and impala) are also prominent. Some of the large grazers incorporate parts of the Kalaharian Zone in their seasonal movements, and the transition to the Kalaharian region is clearly indicated by the presence of both gemsbok and springbok.

The eastern portion of the Transvaalian Zone, known in South Africa as the 'eastern Lowveld', is moister than the western. Bush and tree cover is much denser, and the term 'bushveld' is clearly appropriate. The overall variety of large mammal species is basically the same as to the west, but browsers and mixed feeders are more prominent numerically, as are grazers that prefer more wooded country (roan antelope, sable antelope, and buffalo). Springbok and gemsbok are absent.

The southern extension of the zone is covered by subtropical thornbush and scrub-forest in a subhumid rather than semi-arid setting. In the north, the fauna is very similar to that of the eastern Lowveld. Further to the south, beyond Zululand (KwaZulu), many of the Lowveld species drop out, and the fauna becomes essentially indistinguishable from that of the adjacent part of the Cape Ecozone.

Geomorphic evidence of former very large lakes in the Makarikari and Makgadikgadi Depressions (Street & Grove 1976; Grey & Cooke 1977), as well as interstratified evaporites and aeolian sands in a cave in the Kwihabe Hills of northern Botswana (Grey & Cooke 1977) demonstrate alternation between wetter and drier periods during the Upper Pleistocene and Holocene in the western part of the Transvaalian Zone. Data presented by Heine (1978) suggest that conditions were particularly wet 30 000 to 18 000 and again 11 000 years ago, with arid conditions in between. If this is correct, then long-term precipitation trends in the western part of the Transvaalian Zone may have been out of phase with those immediately to the south in the Kalaharian Zone, where much of the interval between 18 000 and 11 000 B.P. appears to have been very wet (see Heine 1978 and below).

Levels of *éboulis secs* formed by frost weathering in Bushman Rock Shelter and Border Cave in the eastern part of the Transvaalian Zone (Butzer, Beaumont & Vogel 1978) document the intervals of much reduced Upper Pleistocene temperatures apparent in the deep-sea record. The sedimentary fills are not so informative about past precipitation changes, but it appears that there was no one-to-one correspondence between cooler and wetter periods. Sedimentation rates extrapolated from the radiocarbon-dated portion of the Border Cave sequence provide a basis for correlating the temperature fluctuations it records with ones established in the global marine record. The extent of temperature depression involved has not been established, but to the north, at Wolkberg Cave in the north-central Transvaal, the oxygen-isotope ratios of Upper Pleistocene cave carbonates have been used to suggest very tentatively that average temperatures during cold episodes were as much as 8,5–9°C below present ones (Talma *et al.* 1974).

Pollen recovered from peat deposits at Wonderkrater near Naboomspruit in the central Transvaal, indicates that, during at least some cooler phases, Transvaalian bushveld was replaced by open grassveld (Scott & Vogel 1978). It was presumably this kind of vegetational change which encouraged the spread of springbok and blesbok to the Cave of Hearths and Kalkbank, as discussed below.

The Upper Pleistocene and Holocene sites in the Transvaalian Zone that have provided remains of large mammals are listed in Table 3, along with the probable or suggested correlation of sites (or levels within them) with various oxygen-isotope stages. The Transvaalian Zone is second only to the Cape Zone in the number of sites correlated with various stages, but the available faunal samples are mainly small, incompletely described, or both.

The most dramatic changes through time in large mammal species frequencies have been recorded at Melkhoutboom Cave, located at the extreme south-western margin of the Transvaalian Zone, in an area that is transitional to the Cape Zone. Historically, the vegetation near Melkhoutboom was dominated by forest, closed bush, and sclerophyllous scrub, and the most common large mammals were various browsing ungulates—notably bushbuck, kudu, blue duiker, grysbok, and bushpig. The only prominent grazer was the Cape buffalo, which, in spite of its dietary preferences, is known to be very much at home in closed, bushy environmental settings.

The deposits at Melkhoutboom have provided a semi-continuous series of large mammal assemblages dating from approximately 15 400 to 2 000 years ago. The principal species in deposits dated to younger than 7 600 B.P. are the historically prominent browsers and the buffalo. However, in deposits older than

7 600 years, and particularly in ones older than 10 500 years, the browsers and buffalo are rare or absent, and the fauna is dominated by alcelaphine antelopes (black wildebeest, Cape hartebeest, blesbok/bontebok) and equid (either mountain zebra or quagga or both). This assemblage is more reminiscent of the fauna of the Basutolian Zone to the north than of the Transvaalian one in which Melkhoutboom is presently located. More generally, the pre-10 000 B.P. fauna from Melkhoutboom clearly suggests that the environs of the site were grassier in the terminal Pleistocene (late stage 2) than during most of the Holocene (stage 1). The same sort of vegetational change—from grassier to bushier or scrubbier—is reflected in faunal change within late Pleistocene to Holocene sequences at several sites in the near-by Cape Zone, as discussed below. The fact that the faunal change at Melkhoutboom and in the Cape Zone sites is so clear-cut probably reflects their position near the southern margin of the continent where Upper Pleistocene and Holocene environmental changes were perhaps more dramatic than in many areas nearer the Equator.

The basal levels at both Wilton and Uniondale, located not far east of Melkhoutboom, also perhaps date from a time (very early Holocene or terminal Pleistocene) when large grazers were relatively common near-by, but the faunal samples are far too small to document this. At both sites, the bulk of the fauna comes from mid to late Holocene levels, and the principal species represented are the same ones that dominate the contemporaneous deposits at Melkhoutboom—bushpig, bushbuck, duiker, grysbok or steenbok, and Cape buffalo.

An earlier Upper Pleistocene interval broadly comparable to the terminal Pleistocene at Melkhoutboom may be reflected in the fauna from Aloes, also in the transitional area between the Transvaalian and Cape Zones. Land-snail shells associated with the bones at Aloes yielded a radiocarbon age of greater than 37 000 years. The relatively large sample has provided no identifiable bones of browsers, though large grazers (quagga, 'giant Cape horse', wildebeest, common springbok, and warthog) are well represented.

In the heartland of the Transvaalian Zone, far to the north, the available evidence suggests that faunal change related to more general environmental change was more subtle than at Melkhoutboom, but such change did occur. This is particularly clear at Border Cave, which has provided analysable faunal remains from deposits correlated with deep-sea isotope stages 5d through 3. Using the number of squares in which bones of a species occur as an index of its abundance in each Border Cave level, the writer has been able to show that levels in which bushpig, Cape buffalo, tragelaphine antelopes (kudu, nyala, bushbuck, and eland), and impala are relatively common, alternate with levels in which warthog, Burchell's zebra, and alcelaphine antelopes are more prominent.

Warthog, zebra, and alcelaphines were probably more common near by in historic times, and the writer has suggested that levels in which bushpig and buffalo are relatively abundant reflect Upper Pleistocene intervals in which the vegetation contained more bush than in recent times. This conclusion is supported by analysis of the sediments (Butzer, Beaumont & Vogel 1978),

TABLE 3

Upper Pleistocene and Holocene sites that have provided remains of large mammals in the Transvaalian Ecozone.

SITE	GENERAL SOURCE	PERSON IDENTIFYING FAUNA AND SEPARATE PUBLICATION, IF ANY	ARCHAEOLOGICAL ASSOCIATIONS
Isotope Stage 1, late (*c. 5 000–0 B.P.*)			
Onink	Beaumont (pers. comm.)	R. G. Klein	LSA
Embabeni	Beaumont (pers. comm.)	R. G. Klein	LSA
Shongweni (upper occupation)	Davies (1975)	R. G. Klein & P. L. Carter	LSA
Fairview	Robertshaw (pers. comm.)	R. G. Klein	LSA
Ann Shaw (MAJ)	Derricourt (1977)	R. G. Welbourne	LSA
Wilton (levels 1–3F)	J. Deacon (1972)	C. K. Brain	LSA
Melkhoutboom (levels CAF, OMB)	H. J. Deacon (1976)	R. G. Klein	LSA
Isotope Stage 1, early (*c. 12 000–5 000 B.P.*)			
Bushman Rock Shelter	Louw (1969); Eloff (1969); Plug (unpub.)	C. K. Brain (1969*b*); I. Plug	LSA
Heuningsneskrans (layers 3, 2)	Vogel & Marais (1971); Beaumont (pers. comm.)	J. Kitching	LSA
Mlaula	Beaumont (pers. comm.)	R. G. Klein	LSA
Wilton (levels 3G–4)	J. Deacon (1972)	C. K. Brain	LSA
Melkhoutboom (levels MB–RF)	H. J. Deacon (1976)	R. G. Klein	LSA
Isotope Stage 1, undifferentiated (*c. 12 000–0 B.P.*)			
Pomongwe (Pomongwan and Wilton levels)	C. K. Cooke (1963)	C. K. Brain as reported in Sampson (1974)	LSA
Uniondale	M. Brooker (pers. comm.)	R. G. Klein	LSA
Isotope Stage 2 (*c. 32 000–12 000 B.P.*)			
Heuningsneskrans (layer 1)	Vogel & Marais (1971); Beaumont (pers. comm.)	J. Kitching	LSA
Shongweni (lower occupation)	Davies (1975)	R. G. Klein & P. L. Carter	LSA
Melkhoutboom (level B)	H. J. Deacon (1976)	R. G. Klein	LSA
Isotope Stage 3 (*c. 64 000–32 000 B.P.*)			
Border Cave (1BS1r–2BS1rA)	Beaumont *et al.* (1978); Butzer, Beaumont & Vogel (1978)	R. G. Klein (1977)	LSA and MSA
Isotope Stage 4 (*c. 75 000–65 000 B.P.*)			
Border Cave (2 BS1rB, C)	Beaumont *et al.* (1978); Butzer, Beaumont & Vogel (1978)	R. G. Klein (1977)	MSA

(Cont.)

SITE	GENERAL SOURCE	PERSON IDENTIFYING FAUNA AND SEPARATE PUBLICATION, IF ANY	ARCHAEOLOGICAL ASSOCIATIONS
Isotope Stages 3 and 4, undifferentiated (*c. 75 000–32 000 B.P.*)			
Bushman Rock (later MSA levels)	Louw (1969); Eloff (1969); Plug (unpub.); Butzer (in prep.)	C. K. Brain (1969*b*); I. Plug	MSA
Isotope Stage 5a			
Border Cave (2WA, 3BSup)	Beaumont *et al.* (1978); Butzer, Beaumont & Vogel (1978)	R. G. Klein (1977)	MSA
Isotope Stage 5b			
Border Cave (3BS1r, 3WA)	Beaumont *et al.* (1978); Butzer, Beaumont & Vogel (1978)	R. G. Klein (1977)	MSA
Isotope Stage 5d			
Border Cave (1GBSup, 1r)	Beaumont *et al.* (1978); Butzer, Beaumont & Vogel (1978)	R. G. Klein (1977)	MSA
Isotope Stages 3, 4, and/or 5, undifferentiated (*c. 128 000–32 000 B.P.*)			
Pomongwe (MSA layers)	C. K. Cooke (1963)	C. K. Brain as reported in Sampson (1974)	MSA
Chelmer	Bond & Summers (1951)	H. B. S. Cooke & L. H. Wells (1951); H. B. S. Cooke (1963)	none
Bulawayo Waterworks	Zealley (1916)	A. E. V. Zealley & S. Haughton	none
Kalkbank	Mason (1962, 1967); Mason *et al.* (1958)	H. B. S. Cooke (1962); R. G. Welbourne (1971)	MSA
Cave of Hearths	Mason (1962)	H. B. S. Cooke (1962)	MSA
Aloes	Gess (1969)	L. H. Wells (1970*a*)	none

which establishes a general correspondence between apparently colder episodes, as reflected in sediments, and 'bushier' fauna. Unfortunately, the faunal samples from various levels are too small for a truly detailed study of the relationship between changes in sediment parameters and species frequencies.

Yet further north, environments different at one or more times during the Upper Pleistocene from modern ones are probably implied by the presence of common springbok and of blesbok/bontebok at the Cave of Hearths and especially at Kalkbank. Both sites are located north of the areas in which these species were distributed in historic times (Kettlitz 1962). In the vicinity of both sites, the impala apparently fills the niche occupied by the springbok elsewhere, yet in the fossil fauna from Kalkbank, for which species frequency estimates are available, springbok is actually more common than impala. The occurrence of springbok and of bontebok/blesbok in earlier Upper Pleistocene contexts at the Cave of Hearths and Kalkbank was perhaps to be expected in view of their presence in broadly contemporaneous deposits at Redcliff yet further north, and probably reflects the same vegetational change (less bush, more grass) as at Redcliff.

THE KALAHARIAN ECOZONE

This ecozone corresponds broadly to that part of the southern African interior plateau that is often known as the Kalahari desert, though it is not really a desert in either climatic or vegetational terms. With regard to modern political units, the Kalaharian Zone covers eastern South West Africa, the western two-thirds of Botswana, and a large portion of the adjacent (northern) Cape Province of South Africa.

Rainfall in the Kalaharian Zone is erratic and comes almost entirely in summer. The average decreases from roughly 500 mm/a in the north-west to as little as 200 mm in the south-west. Highly porous, sandy soils soak up rainfall rapidly, so that surface water is relatively rare, even in areas where the average rainfall is fairly high. Vegetation cover is highly variable, from relatively luxuriant acacia savanna with an important grass component in the better watered parts (particularly in the north) to sparse shrub acacia savanna and bushveld in the more arid parts (particularly in the south).

At least historically, the grass cover over much of the Kalaharian region was sufficient to support fair numbers of gregarious, migratory grazing ungulates, particularly ones which are capable of obtaining their moisture requirements largely from plants. Springbok and gemsbok were especially common, and blue wildebeest, hartebeest, Burchell's zebra, and warthog were at least locally abundant. Browsing animals, including especially giraffe and greater kudu, were generally less common. Among mixed feeders, eland and steenbok were widespread. Bushbuck (a browser), Cape buffalo and roan antelope (grazers), and impala (a mixed feeder) occurred in some areas of denser bush. Among non-ungulate herbivores, hare(s), springhare, porcupine, baboon, and rock hyrax were (and in some cases still are) widespread and abundant. The principal carnivores preying on these creatures or scavenging on their carcasses were lion, leopard, cheetah, brown hyena, spotted hyena, Cape hunting dog, and jackals.

Upper Pleistocene and Holocene environmental change within the Kalaharian Zone has been best documented by geomorphic research at its south-eastern margin, particularly along the Gaap Escarpment in the northern Cape Province (Butzer, Stuckenrath *et al.* 1978). Alternation of subhumid and semi-arid climatic phases is apparent in the Gaap sequence, with the earliest radiocarbon-dated subhumid phase fixed between $\geq$21 000 and 14 000 years ago. Subsequent subhumid phases are dated between 9 700 and 6 500 B.P. and between 4 500 and 400 B.P. Long-term fluctuations in precipitation appear to be broadly in phase with those recorded in the Basutolian Zone to the east, but not necessarily with those in the Transvaalian Zone to the north (see above and Heine 1978).

Beds of cryoclastic rubble document several past episodes of relatively intense cold along the Gaap Escarpment and presumably throughout the Kalaharian Zone. The most recent very cold interval clearly coincided with deep-sea stage 2. The greatest cold appears to have preceded and followed the marked subhumid phase between $\geq$21 000 and 14 000 B.P., indicating that the relationship between past temperature and precipitation change was a complex one.

The Upper Pleistocene and Holocene sites in the Kalaharian Zone which have provided remains of large mammals are listed in Table 4, along with the probable correlation of the sites (or of levels within them) with various oxygen-isotope stages. Most of the sites are located on the south-eastern margin and date from the late Holocene. The late Holocene faunal samples are dominated by hare(s), springhare, rock hyrax, Burchell's zebra or quagga, warthog, black wildebeest and/or Cape hartebeest, springbok, and steenbok. The mountain reedbuck is also relatively common, reflecting the relatively rugged topography surrounding many of the sites. In no case is there any clear suggestion of an environmental setting that differed significantly from the historic one.

With the important exception of the fauna from Equus Cave, which has been sorted and identified, but not yet analysed, the faunas from Kalaharian sites of Pleistocene age are either small, poorly excavated, incompletely reported, or all three. Most of them are also very imprecisely dated. All this makes it difficult to assess their palaeoenvironmental significance. However, the occurrence of blesbok/bontebok at Black Earth Cave, Witkrans Cave, and especially at Gobabis far to the north-west of the species' historic range, suggests a vegetation cover in which perennial grasses may have played a greater role than they did historically in the Kalaharian region. The occurrence of vaalribbok at Black Earth Cave, Ochre Cave, and Boetsap may have broadly similar implications, depending upon how common it was in the deposits (the samples presently available for study are all highly selected and therefore not suitable for establishing species frequencies). The vaalribbok occurred near all the sites in historic times, but was not especially common. It has so far not been recorded in local

TABLE 4

Upper Pleistocene and Holocene sites that have provided remains of large mammals in the Kalaharian Ecozone.

SITE	GENERAL SOURCE	PERSON IDENTIFYING FAUNA AND SEPARATE PUBLICATION, IF ANY	ARCHAEOLOGICAL ASSOCIATIONS
Isotope Stage 1, late (*c. 5 000–0 B.P.*)			
Witkrans Cave ('Wilton' level)	Peabody (1954)	H. B. S. Cooke (n.d.)	LSA
Little Witkrans	Peabody (1954); Beaumont (pers. comm.)	H. B. S. Cooke (n.d.); R. G. Klein	LSA
Powerhouse Cave	Peabody (1954); Humphreys (1978)	R. G. Klein (1979*a*)	LSA
Limerock 1, 2	Humphreys (in prep.)	R. G. Klein (1979*a*)	LSA
Dikbosch 1, 2	Humphreys (1974, and in prep.)	R. G. Klein (1979*a*)	LSA
Burchell's Shelter	Humphreys (1975)	R. G. Klein (1979*a*)	LSA
Doornfontein	Beaumont & Boshier (1974)	J. Kitching	LSA
Wonderwerk Cave ('later Smithfield')	Beaumont (pers. comm.); Butzer (pers. comm.)	unidentified	LSA
≠gi (LSA level)	Brooks & Yellen (1979)	R. G. Welbourne	LSA
Isotope Stage 1, early (*c. 12 000–5 000 B.P.*)			
Wonderwerk Cave ('earlier Smithfield')	Malan & Cooke (1941); Malan & Wells (1943); Beaumont (pers. comm.); Butzer (pers. comm.)	H. B. S. Cooke & L. H. Wells	LSA
Isotope Stage 1, undifferentiated (*c. 12 000–0 B.P.*)			
Ochre Cave	Peabody (1954)	H. B. S. Cooke (unpub.)	LSA
Isotope Stage 5 (*c. 128 000–75 000 B.P.*)			
Witkrans Cave (MSA levels)	Peabody (1954); Clark (1971); Butzer, Stuckenrath *et al.* (1978)	H. B. S. Cooke (unpub.)	MSA
Equus Cave	Beaumont & Shackley (pers. comm.); Butzer, Stuckenrath *et al.* (1978)	R. G. Klein	none
Gobabis	Jacobson (1978*a*); Butzer (pers. comm.)	R. G. Klein	none
Isotope Stages 3, 4 and/or 5, undifferentiated (*c. 128 000–32 000 B.P.*)			
Black Earth Cave	Peabody (1954)	H. B. S. Cooke (unpub.); R. G. Klein	none
Boetsap	Peabody (1954)	H. B. S. Cooke (unpub.); R. G. Klein	none
Munro's Site (Oppermansdrif faunal locality)	Mason (1969)	R. G. Welbourne (1971)	none
≠gi (MSA level)	Yellen (1971); Helgren (1978); Brooks & Yellen (1979)	R. G. Welbourne	MSA

late Holocene faunas (unless the fauna from Ochre Cave dates from this interval). It is a hillside grazer which is most at home in the Basutolian and Cape Zones, where its frequency in both live communities and archaeological sites tends to be highly correlated with and subequal to that of mountain reedbuck. Moister conditions may well be implied if it were as frequent as mountain reedbuck in a Kalaharian fossil fauna.

THE BASUTOLIAN ECOZONE

This zone comprises the Drakensberg Mountains and the high plateau country adjacent to them. In modern political terms, it covers the southern Transvaal, the western quarter of Swaziland, the highlands of western Natal, all of Lesotho, most of the Orange Free State, and a portion of the adjacent eastern Cape Province. The area is characterized by warm, relatively moist summers (average precipitation generally between 620 and 750 mm) and cold, dry winters. East of the Drakensberg, the historic vegetation of the Basutolian Zone was primarily open grassland with patches of temperate forest at the heads of river valleys and areas of acacia savanna at lower altitudes. West of the Drakensberg, in the area known in South Africa as the 'highveld', the vegetation was nearly pure grassveld with trees largely confined to the river valleys.

Historically, the fauna of the Basutolian region was dominated overwhelmingly by large, migratory, gregarious grazers, especially Burchell's zebra, the recently extinct quagga, black wildebeest, blesbok, and springbok. Their numbers may even have exceeded those of their counterparts in the east African grasslands, and it is probable that they were interdependent in a grazing succession similar to that recently observed in east Africa. They probably migrated with the seasons in search of good pasture, and it is likely the migrations took in the eastern part of the Karoo–Namaqualian Zone into which the Basutolian one merges imperceptibly.

In keeping with the open nature of the vegetation, browsers (greater kudu, bushbuck, etc.) and grazers favouring wooded country (roan, sable, Cape buffalo) were rare or absent in the Basutolian Zone. The impala was completely displaced by the springbok, but eland and steenbok, also mixed feeders, were widespread. Warthogs were numerous, but bushpigs were generally absent. Mountain reedbuck, vaalribbok, and to a lesser extent klipspringer were common in areas of high relief. Among smaller mammals, hares, springhare, and rock hyrax are still abundant in many places.

Pollen-analytical studies undertaken at Florisbad by Van Zinderen Bakker (1957) and at Aliwal North by Coetzee (1967), both located near the western margin of the Basutolian Zone, reveal that the local grassveld was replaced at various times in the later Pleistocene by semi-desert shrub of the Karoo-Namaqualian Zone. At Aliwal North, where the sequence is reliably dated between approximately 13 200 and 9 600 B.P., a replacement of grassveld by Karoo shrub (and the reverse) occurred three times, reflecting relatively rapid fluctuations between cooler/moister and warmer/drier conditions similar to the kind of relatively rapid climatic fluctuations that are known to have characterized the contemporaneous terminal Pleistocene/Holocene transition in Europe.

At Florisbad, the pollen spectra are all much older and precise dating is a problem, though a grassveld phase indicating relatively moist conditions occurs in deposits that probably correlate with deep-sea isotope stage 2. Studies of alluvial cut-and-fill sequences in the Upper Orange drainage by Butzer (1971*b*) also indicate that stage 2 times were generally wet in the Basutolian Zone, as they were in the neighbouring Kalaharian one. Yet earlier wetter and drier phases are difficult to date, and it is clear that the ones reflected in pollen spectra at Florisbad are beyond the range of radiocarbon. The earliest part of the Florisbad sequence, in fact, probably dates from the later mid-Pleistocene.

The Upper Pleistocene and Holocene sites in the Basutolian Zone which have provided remains of large mammals are listed in Table 5, along with the probable correlation of the sites (or of levels within them) with various oxygen-isotope stages. Most of the sites are located near the western margin of the zone and either date very clearly from the late Holocene or are difficult to date precisely.

The late Holocene faunas are dominated by hare(s), rock hyrax, Burchell's zebra and/or quagga, black wildebeest, springbok, and steenbok, suggesting an environment broadly similar to the historic one. Faunas coming from sites located in more rugged topography are clearly marked by a higher frequency of mountain reedbuck and vaalribbok, as would be expected.

The pre-Holocene faunas are also dominated by large gregarious grazers, suggesting general limits to the extent of later Pleistocene environmental change. However, the presence of lechwe or waterbuck at Vlakkraal and Koffiefontein, of Cape buffalo at Koffiefontein and Driefontein, of impala at Koffiefontein, and of roan at Driefontein, may reflect moister conditions at one or more times during the earlier Upper Pleistocene. The lechwe is also present at Florisbad, but its stratigraphic provenience within the site is unknown. It may have come either from Upper Pleistocene levels, from levels that probably date to the late mid-Pleistocene, or from both. The same problems of provenience, reflecting relatively uncontrolled excavations, make it impossible to relate various elements in the Florisbad fauna to the palynological and geomorphic observations that have been made at the site, but the fauna is further interesting for the presence of hippopotamus, suggesting a time(s) when the pan next to the site may have contained a lake. The occurrence of water mongoose and clawless otter may reflect the same moist interval(s). Perhaps even more intriguing is the occurrence of giraffe, which must indicate that trees once grew near by, though the area was treeless historically, and Van Zinderen Bakker found virtually no arboreal pollen in any of the samples he examined from the site.

THE KAROO–NAMAQUALIAN ECOZONE

This zone has two major components: (i) the Namib Desert, a narrow strip up to 160 km wide along the Atlantic coast, extending from the mouth of the Orange River through South West Africa to beyond Mossamedes in Angola;

TABLE 5

Upper Pleistocene and Holocene sites that have provided remains of large mammals in the Basutolian Ecozone.

SITE	GENERAL SOURCE	PERSON IDENTIFYING FAUNA AND SEPARATE PUBLICATION, IF ANY	ARCHAEOLOGICAL ASSOCIATIONS
Isotope Stage 1, late (c. 5 000–0 B.P.)			
Driel Shelter	Maggs (pers. comm.)	R. G. Klein	LSA
Moshebi's Shelter	Carter (1969, 1977); Carter & Vogel (1974)	P. L. Carter	LSA
Melikane	Carter (1977)	P. L. Carter	LSA
Sehonghong	Carter (1977); Carter & Vogel (1974)	P. L. Carter	LSA
Belleview	Carter (1977)	P. L. Carter	LSA
Rose Cottage Cave	Malan (1952); Butzer (pers. comm.)	unidentified	LSA
Ventershoek	Sampson (1970)	R. G. Klein (1979*a*)	LSA
Holmsgrove	Sampson (1970)	unidentified	LSA
Zaayfontein	Sampson (1967*a*, 1970)	J. Kitching	LSA
Riversmead	Sampson & Sampson (1967)	R. G. Klein (1979*a*)	LSA
Glen Elliott Shelter	Sampson (1967*b*)	R. G. Klein (1979*a*)	LSA
Blydefontein	Sampson (1970)	R. G. Klein (1979*a*)	LSA
Tafelberg Hall	Hewitt (1931)	?	LSA
Highlands Shelter	H. J. Deacon (1976)	R. G. Klein	LSA
Isotope Stage 2 (c. 32 000–12 000 B.P.)			
Sehonghong	Carter (1977); Carter & Vogel (1974)	P. L. Carter	LSA
Florisbad (Peat III)	Dreyer (1938); Hoffman (1955); Meiring (1956); Butzer (1971*b* and pers. comm.)	H. B. S. Cooke & Wells; H. B. S. Cooke (1963)	?
Isotope Stage 5 (c. 128 000–75 000 B.P.)			
Florisbad (Peat II)	Dreyer (1938); Hoffman (1955); Meiring (1956); Butzer (1971*b* and pers. comm.)	H. B. S. Cooke & Wells; H. B. S. Cooke (1963)	?MSA
Vlakkraal	Wells *et al.* (1942); Butzer (1971*b*; and pers. comm.)	H. B. S. Cooke & Wells; H. B. S. Cooke (1963)	MSA
Koffiefontein	H. B. S. Cooke (1948); Butzer (1971*b*; and pers. comm.)	H. B. S. Cooke	?
Isotope Stages 3, 4 and/or 5, undifferentiated (c. 128 000–32 000 B.P.)			
Melikane	Carter (1977)	P. L. Carter	MSA
Sehonghong	Carter (1977); Carter & Vogel (1974)	P. L. Carter	MSA
Driefontein	Wells (1970*b*)	L. H. Wells; R. G. Klein (1974*a*)	?MSA

and (ii) the Karoo, a great plain stretching across the Cape Province from the Orange River on the north to the Cape Folded Mountains on the south.

The Namib is the most extreme desert in southern Africa. Average rainfall within it nowhere exceeds 130 mm/a, and there are many places where it is less than 25 mm. Vegetation is largely confined to the major river valleys, except after occasional rains when stands of annual grasses briefly appear. The southern part of the Namib (south of the Kuiseb River) is a dune sea, while the northern part consists primarily of gravel plains and barren, rocky hills. The principal large mammals in the desert proper are gemsbok and springbok, supplemented by rock hyrax, hares, steenbok, klipspringer, and mountain zebra in some hillier parts and on the dissected escarpment that separates the desert from the Kalaharian Zone to the east.

The Karoo is less arid than the Namib, with average rainfall varying between 130 and 400 mm/a, depending on the place. Over most of the Karoo, rain comes primarily in summer, but in the south-western parts, as much as half may come in winter. Typical Karoo vegetation is low scrub with much bare ground in between and a sparse scattering of grasses. Trees, consisting mainly of acacias, are confined to the river valleys. The density of grass increases towards the east, until the Karoo merges more or less imperceptibly with the grassveld of the Basutolian region. The most common large mammals in the Karoo were probably rock hyrax, hare(s), springbok, gemsbok, black wildebeest, steenbok, grey duiker, and quagga.

Hard evidence for Upper Pleistocene and Holocene environmental change in the Karoo–Namaqualian Zone is sparse and has been summarized by Coetzee (1978*a*). Geomorphic features pointing to once wetter conditions, even in the Namib, are relatively widespread, but the dates of the wetter periods remain unestablished.

The Upper Pleistocene and Holocene sites in the Karoo–Namaqualian Zone that have provided remains of large mammals are listed in Table 6, along with the probable correlation of the sites (or of levels within them) with various oxygen-isotope stages. The sites are divisible into two basic groups: to the north, a series of rock shelters in hilly areas adjacent to the Namib Desert, and to the south, Elands Bay Cave in a part of the Karoo that is transitional to the Cape Zone. Fossiliferous Upper Pleistocene or Holocene sites within the Karoo or Namib proper are virtually unknown so far, excepting some very recent coastal middens yielding mainly remains of pinnipeds (Jacobson & Klein unpub.; Thackeray 1975, 1979), Mirabib Rock Shelter, from which only the microfauna has been identified (Sandelowsky 1974, 1977; Brain & Brain 1977), and 'Namib 2', a locality just south of the Kuiseb recently discovered by Shackley (pers. comm.).

The hilly, rocky topography surrounding the sites located on the margins of the Namib is clearly reflected in their faunas, in which rock hyrax and klipspringer are very common. Hares, an equid that is probably mountain zebra, springbok, and steenbok are also relatively well represented. Although some

TABLE 6

Upper Pleistocene and Holocene sites that have provided remains of large mammals in the Karoo–Namaqualian Ecozone.

SITE	GENERAL SOURCE	PERSON IDENTIFYING FAUNA AND SEPARATE PUBLICATION, IF ANY	ARCHAEOLOGICAL ASSOCIATIONS
Isotope Stage 1, late (*c. 5 000–0 B.P.*)			
Brandberg Sites (Lower Numas Cave, Orabes Shelter 4, Tirara Shelter, Girls' School Shelter)	Jacobson (1978*b*)	R. G. Klein	LSA
Fackelträger	Wendt (1972); Thackeray (1979)	C. K. Brain	LSA
Big Elephant Shelter	Wadley (1976, 1979)	R. G. Klein	LSA
Striped Giraffe Shelter	Wadley (1979)	I. Plug (1979)	LSA
Nos	Wendt (unpub.)	F. Thackeray (1979)	LSA
Namtib	Wendt (1972)	F. Thackeray (1975, 1979)	LSA
Tiras 5	Wendt (1972)	F. Thackeray (1975, 1979)	LSA
Haalenberg	Wendt (unpub.); Thackeray (1979)	R. G. Klein	LSA
Aar I and II	Wendt (1972)	F. Thackeray (1975, 1979)	LSA
Pockenbank (LSA)	Wendt (1972)	F. Thackeray (1975, 1979)	LSA
Apollo 11 ('Pottery LSA')	Wendt (1972)	F. Thackeray (1975, 1979)	LSA
Elands Bay Cave (levels 1–9)	Parkington (1972, 1976, 1978, n.d.)	R. G. Klein	LSA
Isotope Stage 1, early (*c. 12 000–5 000 B.P.*)			
Apollo 11 ('Wilton')	Wendt (1972, 1976)	F. Thackeray (1975, 1979)	LSA
Elands Bay Cave (levels 17–10)	Parkington (1972, 1976, 1978, n.d.)	R. G. Klein	LSA
Isotope Stage 2 (*c. 32 000–12 000 B.P.*)			
Apollo 11 ('Early LSA')	Wendt (1972, 1976)	F. Thackeray (1975, 1979)	LSA
Elands Bay Cave (levels 20–18)	Parkington (1972, 1976, 1978, n.d.)	R. G. Klein	LSA
Isotope Stages 3 and/or 4, undifferentiated (*c. 75 000–32 000 B.P.*)			
Apollo 11 ('Blade MSA')	Wendt (1972, 1976)	F. Thackeray (1975, 1979)	MSA
Pockenbank (MSA)	Wendt (1972)	F. Thackeray (1975, 1979)	MSA
Isotope Stage 5 (*c. 128 000–75 000 B.P.*)			
Apollo 11 ('Crescent MSA' and Older MSA)	Wendt (1972, 1976)	F. Thackeray (1975, 1979)	MSA

of the samples clearly date from Upper Pleistocene intervals in which climatic conditions were certainly different from modern ones, there is no faunal evidence for a significantly different past environment. The reason is perhaps small sample size more than a real lack of Upper Pleistocene faunal and environmental change.

Elands Bay Cave is located on the Atlantic coast, far south of the other sites, in an area that is transitional between the Karoo–Namaqualian and Cape Zones. The cave has provided relatively large faunal assemblages bracketed between roughly 17 000 B.P. and the historical present, though there is a major gap in the sequence from approximately 8 000 to 4 000 B.P. Large grazing ungulates are relatively more common in levels ante-dating 9 000 B.P., suggesting that grasses were relatively more important near by in the late Pleistocene than in the Holocene. The same kind of faunal change, probably also reflecting a reduced role for grasses in the Holocene, is even more apparent at sites located within the near by Cape Zone. An increase in the frequency of steenbok relative to grysbok in Elands Bay levels postdating 9 000 B.P. perhaps reflects subtle, but locally significant, changes in the nature of the non-grass component of the vegetation near the site.

Like coastal sites in the Cape Zone that contain a comparable late Pleistocene/Holocene sequence, Elands Bay further records the terminal Pleistocene/early Holocene rise in sea-level. During the period of much depressed sea-levels between 17 000 and 12 000 years ago, the coastline was always more than 10 km from the site, and remains of marine creatures are very rare in deposits dating from this interval. By 11 000 B.P., the coastline had probably moved to within 4 km of the site, and most kinds of edible marine creatures, prominently including the Cape fur seal, first appear in deposits of about this age. By 9 000 B.P. or so, the coast was in approximately its present position, and remains of marine species are superabundant in all the younger levels.

THE CAPE ECOZONE

By far the smallest of the ecozones considered here, this zone consists of the Cape Folded Mountains and the adjacent coastal plains. The mountains set it off from the Karoo–Namaqualian Zone to the north, and a spur of the mountains reaching the sea at Cape Hangklip separates the coastal plain into two usefully distinguished parts—the south-western Cape and the southern Cape. The south-western Cape has a typically Mediterranean climate, with wet, cool winters and hot, dry summers. The southern Cape is also marked by strong seasonal contrasts in temperatures, but rainfall tends to be more evenly distributed throughout the year, especially to the east.

The vegetation typical of much of the Cape Ecozone is known locally as fynbos and bears a broad resemblance to the macchia of the Mediterranean region. Typical fynbos plants are shrubs of various kinds with small, hard leaves that are capable of withstanding summer drought. The principal families are reeds (Restionaceae), heaths (Ericaceae), and proteas (Proteaceae). Irises and orchids (*sensu lato* Iridaceae and Orchidaceae) are common, but grasses (Gramineae) are relatively rare. At least historically, the higher slopes of the mountains in the western part of the region bore forests of 'cedar' (*Widdringtonia*), while the lower mountain slopes and adjacent coastal plain in the south-eastern part of the zone, centred roughly on the town of Knysna, carried a mixed forest of yellowwood and evergreen broadleaf trees. Smaller stands of essentially the same kind of mixed forest occurred in relatively moist, sheltered microenvironments elsewhere in the Cape Zone as well.

Reflecting the nature of the vegetation, at least historically the fauna of the Cape Ecozone was dominated by browsing ungulates. In the southern Cape, the principal browsers were bushpig, bushbuck, blue duiker, grey duiker, and Cape grysbok. Among the grazers, only the Cape buffalo was common more or less throughout. Hartebeest was locally fairly numerous. Bontebok and blue antelope, though entirely restricted (endemic) to this region were rare, and the blue antelope became extinct about 1800 A.D. Roan antelope occurred in small numbers in the forests of the south-east. Eland and steenbok (mixed feeders) occurred more or less throughout, though the steenbok was probably completely replaced by the grysbok in areas of dense fynbos, bush, or forest. Vaalribbok and mountain reedbuck were common in suitably hilly locales, particularly in the flanking Cape Mountains, where they were joined by the mountain zebra. The most common non-ungulate herbivores were baboons, rock hyraxes, porcupines, and hares. On the west, a large endemic mole-rat (*Bathyergus suillus*) was also abundant in sandy, mainly coastal areas. Cape fur seal was common in coastal waters, and rookeries even occurred on the mainland.

The fauna of the south-western Cape was similar, but more impoverished, lacking bushpig, bushbuck, blue duiker, buffalo, mountain reedbuck, blue antelope, roan, bontebok, and other species found in the southern Cape. Grey duiker was relatively abundant and steenbok was generally more common than grysbok. The available faunal evidence suggests less contrast between the south-western and southern Cape during the late Pleistocene, probably in part because of greater climatic similarity and in part because faunal interchange was facilitated by exposure of the continental shelf during periods of lowered sea-level.

In the southern Cape, colder intervals during the Upper Pleistocene are clearly recorded in layers of frost-fractured debris at Nelson Bay Cave (Butzer 1973) and Die Kelders Cave 1 (Tankard 1976; Tankard & Schweitzer 1976), near both of which frost is unknown at present. Butzer's geomorphic research (Butzer & Helgren 1972; Butzer, Stuckenrath *et al.* 1978) suggests that the colder intervals were mainly drier, perhaps in large part because of the greater atmospheric stability promoted by weakening of the warm Agulhas Current off the southern Cape coast. A drier climate during colder intervals in the southern Cape is also indicated by Avery's (in prep.) analysis of the microfauna from Boomplaas Cave A.

Butzer has further detected a shift in geomorphic processes in the southern

Cape at about 4 200 B.P., reflecting relatively drier conditions in the early Holocene and more mesic ones subsequently. Pollen analysis of a Holocene sedimentary sequence at Groenvlei on the coastal fringe of the evergreen forest near Knysna may be read to support generally drier conditions in the early Holocene (Martin 1968).

The nature of Upper Pleistocene and Holocene environmental change in the south-western Cape is much less clearly established, and at least one of the Upper Pleistocene cold intervals may have been significantly moister, permitting the growth of yellowwood forest in areas today covered by sclerophyllous scrub (Schalke 1973; Coetzee 1978*b*).

The Upper Pleistocene and Holocene sites that have provided remains of large mammals in the Cape Ecozone are listed in Table 7, along with the probable correlation of the sites (or of levels within them) with various oxygen-isotope stages. Although it is the smallest of the southern African ecozones discussed here, the Cape Zone contains the largest number of large, reasonably well-dated Upper Pleistocene and Holocene faunal samples, permitting a much more penetrating search for relationships between faunal change and environmental change established on other grounds.

In every Cape site that has provided large, thoroughly analysed late Pleistocene and Holocene faunal assemblages (Byneskranskop 1, Buffelskloof, Boomplaas, and Nelson Bay), the late Pleistocene assemblages contain a significantly higher proportion of large grazing ungulates, particularly alcelaphine antelopes and equids, suggesting that grasses were substantially more important in the regional vegetation during the late Pleistocene. The contrast is especially stark at Nelson Bay Cave, located on the coastal margin of the Knysna Forest, in an area where the principal ungulates recorded historically were bushpig, bushbuck, grysbok, and Cape buffalo. These are also the principal ungulate species in the Nelson Bay deposits postdating 11 000–10 000 B.P. Wildebeest, bontebok, springbok, quagga, and warthog were not present historically near the site and have not been found in deposits there that are younger than 11 000 years, yet they are the dominant species in deposits dating between 18 500 and 12 000 B.P. (the oldest fossiliferous ones at the site). This is probably the least equivocal faunal evidence for environmental change so far found at any Quaternary site in southern Africa. The presence of grassland interspersed with or largely in place of forest at Nelson Bay in the terminal Pleistocene is entirely compatible with Butzer's inference, based on geomorphic observations, that the terminal Pleistocene climate of the southern Cape was drier than the present one.

The faunas from earlier Upper Pleistocene cool or cold intervals also suggest a vegetation cover in which grasses were far more important than they were historically or than in intervening warmer intervals. The most important earlier Upper Pleistocene sites are the complex of caves at Klasies River Mouth, occupied by Middle Stone Age people shortly after a high sea-level which may be correlated with isotope stage 5e. This sea-level is clearly recorded in a beach deposit on bedrock at Klasies Cave 1. On the basis of an analysis of the overlying Klasies sediments, especially the sand component, Butzer (1978*a*) has been able to establish the relationship between subsequent earlier Upper Pleistocene changes in sea-level (as reflected in the fluctuating distance between the sea and the site) and successive Middle Stone Age occupations. The sea-level changes were presumably of glacio-eustatic origin and therefore reflect global climatic events that are also reflected in the deep-sea oxygen-isotope stratigraphy. Oxygen-isotope determinations on (culturally accumulated) marine shells from various Klasies layers in fact indicate the expected correlation between higher off-shore water temperatures and higher sea-levels, as inferred by Butzer, and between cooler off-shore waters and lower sea-levels.

The Klasies sites are located on the eastern edge of the Knysna Forest, where the historic vegetation was a mosaic of evergreen forest, fynbos, and scrub in which the principal ungulates were Cape grysbok, blue duiker, bushbuck, bushpig, and Cape buffalo, much the same as at Nelson Bay, though unlike at Nelson Bay, the Cape hartebeest probably also occurred near by in fair numbers. In any case, the historically common ungulates clearly dominate the late Holocene deposits at Klasies and are also abundant in those earlier Upper Pleistocene layers formed when sea-level was high. In those earlier Upper Pleistocene levels formed when sea-level was low, wildebeest, bontebok, and an equid that is probably quagga are proportionately much more abundant, recalling the terminal Pleistocene fauna at Nelson Bay. Unfortunately, there is a large gap in the Klasies sequence from perhaps 65 000 to 5 000 B.P., so that the record of Upper Pleistocene faunal fluctuations near the site is not complete. Still, the fact that the faunal fluctuations which have been established correlate closely with environmental fluctuations established on other grounds and that they occur in a cultural context very different from that of Nelson Bay, clearly indicates that it was environment and not culture which was ultimately responsible for the faunal changes.

At Die Kelders Cave 1, the oldest stratigraphic unit is a boulder beach recording a sea-level not very different from the modern one. The beach is overlain by sterile quartzose sands overlain in turn by the first Middle Stone Age occupation. This earliest Middle Stone Age layer and a sterile layer immediately above it contain numerous angular, spalled flakes of roof rock that resulted from alternate freezing and thawing under much cooler climatic conditions than the modern ones (Tankard & Schweitzer 1976; Tankard 1976). Frost-fractured debris is also present in higher-lying Middle Stone Age layers, though less common, perhaps because fissures suitable for moisture penetration in the roof were largely removed by the initial freeze-thaw episode. Whatever the case, it is clear that much, if not all of the occupation of Die Kelders by Middle Stone Age people coincided with a distinctly cold interval, correlated here with oxygen-isotope stage 4 and perhaps part of 3, and the faunal sample is relatively rich in gregarious grazers, including some that were not recorded near the site historically and that have not been found in local Holocene faunas, including the one

TABLE 7

Upper Pleistocene and Holocene sites that have provided remains of large mammals in the Cape Ecozone.

SITE	GENERAL SOURCE	PERSON IDENTIFYING FAUNA AND SEPARATE PUBLICATION, IF ANY	ARCHAEOLOGICAL ASSOCIATIONS
Isotope Stage 1, late (c. 5 000–0 B.P.)			
De Hangen	Parkington & Poggenpoel (1971)	Q. B. Hendey, G. Avery, R. G. Klein	LSA
Paternoster	Robertshaw (1977)	R. G. Klein	LSA
Duiker Eiland	Robertshaw (in prep.)	R. G. Klein	LSA
Langebaan Lagoon	Robertshaw (1978)	R. G. Klein	LSA
Gordon's Bay Midden	Van Noten (1974)	A. Gautier	LSA
Die Kelders 1 (LSA levels)	Schweitzer (1970, 1974, 1975); Schweitzer & Scott (1973)	R. G. Klein & K. Scott	LSA
Byneskranskop Cave 1 (levels 1–5)	Schweitzer & Wilson (1978)	R. G. Klein (in press)	LSA
Buffelskloof (BOL)	Opperman (1978)	R. G. Klein (1978*b*)	LSA
Boomplaas (DGL–FBL)	H. J. Deacon (1979); H. J. Deacon & Brooker (1976); H. J. Deacon *et al.* (1976, 1978)	R. G. Klein (1978*c*)	LSA
Nelson Bay Cave (Inskeep excavations)	Inskeep (1965, 1972)	R. G. Klein	LSA
Matjes River Mouth (layers A, B)	Louw (1960)	?	LSA
Andrieskraal 1	J. Deacon (1965)	Q. B. Hendey (Hendey & Singer 1965)	LSA
Andrieskraal 2	J. Deacon (1965)	Q. B. Hendey (Hendey & Singer 1965)	none
Scott's Cave	H. J. Deacon & J. Deacon (1963); H. J. Deacon (1967)	R. G. Klein & K. Scott (1974)	LSA
Klasies River Mouth (Cave 1/1–12; Cave 1D Cave 5/1–2)	Wymer & Singer (1972); Butzer (1978*a*)	R. G. Klein (1976*a*)	LSA
Isotope Stage 1, early (c. 12 000–5 000 B.P.)			
Byneskranskop 1 (levels 19–6)	Schweitzer & Wilson (1978)	R. G. Klein (in press)	LSA

Buffelskloof (HE–MDA)	Opperman (1978)	R. G. Klein (1978*b*)	LSA
Boomplaas (BRL7YA–BRL)	H. J. Deacon (1979); H. J. Deacon & Brooker (1976); H. J. Deacon *et al.* (1976, 1978)	R. G. Klein (1978*c*)	LSA
Nelson Bay Cave (GSL–IC)	Klein (1972*a*, 1972*b*); J. Deacon (1978)	R. G. Klein	LSA
Matjes River Mouth (layers C–E)	Louw (1960)	?	LSA
Isotope Stage 1, undifferentiated (*c. 12 000–0 B.P.*)			
Oakhurst Cave	Goodwin *et al.* (1938); Fagan (1960); Schrire (1962)	L. H. Wells (1960); R. G. Klein	LSA
Glentyre Shelter	Fagan (1960)	L. H. Wells (1960)	LSA
Kangkara Cave	H. J. Deacon & Klein (unpub.)	R. G. Klein	LSA
Isotope Stage 2 (*c. 32 000–12 000 B.P.*)			
Boomplaas (BP–BRL7Y)	H. J. Deacon (1979); H. J. Deacon & Brooker (1976); H. J. Deacon *et al.* (1976, 1978)	R. G. Klein (1978*c*)	LSA and ?MSA
Nooitgedacht 1, 2	J. Deacon (1979)	J. Brink & R. G. Klein	none
Nelson Bay Cave (YGL–BSL)	Klein (1972*a*, 1972*b*); J. Deacon (1978)	R. G. Klein	LSA
Isotope Stages 3 and/or 4, undifferentiated (*c. 75 000–32 000 B.P.*)			
Die Kelders Cave 1 (MSA layers)	F. R. Schweitzer (pers. comm.); T. P. Volman (in prep.); Tankard & Schweitzer (1974, 1976)	R. G. Klein (1975*a*)	MSA
Isotope Stage 5a			
Klasies River Mouth (Cave 1/13, Cave 1A/1–9)	Wymer & Singer (1972); Butzer (1978*a*)	R. G. Klein (1976*a*)	MSA
Isotope Stage 5b			
Klasies River Mouth (Cave 1A/10–21)	Wymer & Singer (1972); Butzer (1978*a*)	R. G. Klein (1976*a*)	MSA
Sea Harvest Faunal localities	Hendey (1974); Northey (1979)	Q. B. Hendey; R. G. Klein; L. Northey	none

SITE	GENERAL SOURCE	PERSON IDENTIFYING FAUNA AND SEPARATE PUBLICATION, IF ANY	ARCHAEOLOGICAL ASSOCIATIONS
Isotope Stage 5c			
Klasies River Mouth (Cave 1/14–37; Cave 1B/1–15; Cave 1C/36–37; Cave 5/5–7)	Wymer & Singer (1972); Butzer (1978*a*)	R. G. Klein (1976*a*)	MSA
Linkerhandsgat-East and Windheuvel (Stanford)	H. B. S. Cooke (1955); Butzer (pers. comm.)	H. B. S. Cooke; R. G. Klein	none
Isotope Stage 5d			
Klasies River Mouth (Cave 1/38–39)	Wymer & Singer (1972); Butzer (1978*a*)	R. G. Klein (1976*a*)	MSA
Swartklip 1	Hendey & Hendey (1968); Klein (1975*c*); Butzer (in prep.)	Q. B. Hendey & R. G. Klein	none
Isotope Stage 5e			
Lake Pleasant (Groenvlei)	Butzer & Helgren (1972); Butzer (pers. comm.)	R. G. Klein	none
Isotope Stage 5, unsubdivided			
Herolds Bay	Brink & Binneman (unpub.); J. Deacon (1979)	Q. B. Hendey & J. Brink	none
Isotope Stages 3, 4 and/or 5, undifferentiated (*c. 128 000–32 000 B.P.*)			
Elandsfontein (in part)	Q. B. Hendey (1974); Inskeep & Hendey (1966)	Q. B. Hendey; L. H. Wells; A. W. Gentry; E. S. Vrba; R. G. Klein; R. Singer *et al.*	?MSA (in part) none (in part)
Bloembosch (possibly pre-5)	H. B. S. Cooke (1955)	H. B. S. Cooke; R. G. Klein	?
Hoedjies Punt 1, 2	Northey (1979)	R. G. Klein; L. Northey	none
Ysterfontein	G. Avery & Scott (unpub.); Northey (1979)	R. G. Klein; L. Northey	none
Duinefontein 1	R. G. Klein (unpub.)	R. G. Klein (incomplete study)	none
Duinefontein 4	R. G. Klein (unpub.); Northey (1979)	R. G. Klein; L. Northey	none
Boomplaas (OLP–LOH)	H. J. Deacon (1979); H. J. Deacon & Brooker (1976); H. J. Deacon *et al.* (1976, 1978)	R. G. Klein (1978*c*)	MSA

from Die Kelders. As at Klasies, the Holocene fauna from Die Kelders dates from the later Holocene, and is unfortunately separated from the Middle Stone Age fauna by an occupation gap spanning several tens of thousands of years.

Finally, analysis of the aeolianite sequences at both Swartklip and Sea Harvest (Butzer pers. comm.) has indicated that the bone accumulations at both sites were formed during periods of lowered sea-level, in each instance probably reflecting major cool intervals within isotope stage 5. In historic times, the principal ungulates near each site were browsers and mixed feeders, but their fossil faunas are heavily dominated by grazers, many of which did not occur in the Cape Zone historically. The implication of a greater role for grasses is clear once again, and the fact that the faunal accumulations at both sites result from carnivore (v. human) activity further supports the notion that the long-term changes in the grazer/browser ratios described for Klasies, Nelson Bay, and other Cape Zone archaeological sites basically reflect changing environments and not changing cultural preferences and practices.

Besides Swartklip and Sea Harvest, there are several other probable carnivore sites in the south-western Cape in which the faunas are dominated by large grazers (Duinefontein 1 and 4, Elandsfontein 'bone circle', Ysterfontein, Hoedjies Punt 1 and 2), but these sites have not been firmly dated on independent grounds. They have therefore not been considered in greater detail here. The fact that grazer-dominated fossil faunas should be so common probably reflects the fact that climatic conditions cooler than present ones occupied much more of Upper Pleistocene time than conditions similar to present ones.

In the southern Cape, there is also one probable carnivore site (at Lake Pleasant) in which the fauna comes from deposits correlated with a warmer interval on independent geomorphic grounds, and although the faunal sample is small, it is probably significant that it contains no alcelaphine antelopes or equids, but that Cape buffalo is represented and dolphin is present, indicating proximity of the sea. The fauna from Bloembos near Darling in the south-western Cape may also date from a warmer interval(s), though possibly a mid rather than Upper Pleistocene one. The Bloembos fauna is especially interesting because it contains the only Pleistocene record of a giraffe in the Cape Zone, and Bloembos is presently located in an area where trees were unknown historically. By itself, giraffe implies a very different environment from the recent one.

One apparent anomaly in all the Upper Pleistocene faunas of the Cape Zone that are especially rich in grazing ungulates is the rarity or absence of steenbok, though grysbok is always present (Klein 1975*b*). Steenbok is much better represented in the browser-dominated Holocene and historic faunas of the region, especially in the south-western Cape, where it often outnumbers grysbok locally. This seems the opposite of what would be expected, since, between the two, it is the steenbok which eats more grass and which might therefore have profited more from grassier vegetation. However, the steenbok is also highly dependent on browse, and the answer to the puzzle is probably the nature of the available browse during cooler, grassier intervals. The grysbok is basically a Cape Zone endemic, and its evolutionary origins and history may well be linked to its ability to make maximum use of those browse plants which remained during the substantial periods when grasses became more common as a result of climatic change. Details of the browse preferences of grysbok v. steenbok in areas where they overlap today might well provide clues as to what browse plants disappeared or became much rarer during Pleistocene cold intervals. More generally, when they can be distinguished osteologically, fluctuations in the relative frequencies of closely related pairs of species such as steenbok and grysbok probably have considerable potential for providing fine detail on past environmental changes.

Klasies, Nelson Bay, Die Kelders, Swartklip, and Sea Harvest are all coastal sites whose faunal contents could be expected to reflect Upper Pleistocene and Holocene changes in sea-level. The late Pleistocene/early Holocene rise in sea-level is, in fact, very clearly reflected in the Nelson Bay sequence in which shells or bones of marine animals do not occur in the deposits dating to between 18 500 and 12 000 B.P. Marine creatures, including the Cape fur seal, appear only in deposits dated to about 12 000, when the coastline had moved to within 10 km of the site, and they become especially abundant in deposits younger than 10 000 B.P., after which the sea was always within easy striking distance. The same phenomenon is recorded in the terminal Pleistocene/early Holocene sequence at Byneskranskop 1, though seal bones are less common throughout, presumably because the site has never been directly on the coast (it is presently about 6 km away).

The marine regressions that occurred during the earlier Upper Pleistocene (Middle Stone Age) occupations at Klasies River Mouth are known to have been less dramatic than the terminal Pleistocene one, and this is apparently reflected in the presence of seal bones and other marine food debris throughout the Klasies sequence. There is, however, a tendency for seals to be less well represented in layers formed during regressive phases. Less dramatic regression, in combination with a steeply sloping continental shelf immediately off shore at Die Kelders, is perhaps also responsible for the occurrence of seal bones throughout the Middle Stone Age occupation there. It is probably significant that seal bones are less common in the Middle Stone Age levels than in the late Holocene ones, formed when the sea lapped virtually at the mouth of the cave, as it does today.

At Swartklip, marine creatures are completely absent, perhaps implying a more substantial regression than at Sea Harvest where seals and other marine creatures are represented in small quantities. Again, the continental shelf immediately off Sea Harvest is relatively steep, so that substantial regression would be necessary to remove the sea completely from the rounds of its (?)hyaena inhabitants. It is interesting that where seal bones do occur in Cape Zone deposits apparently dating from a relatively cool interval, antarctic and subantarctic seals (especially elephant seal, but also gazelle seal and crab-eater) appear to be relatively better represented than in deposits from warmer intervals in which Cape fur seal is often the only pinniped present.

The relatively large faunal samples available from the Holocene levels at Nelson Bay are less different from one another than are any of them from the late Pleistocene samples, but they are still characterized by significant change through time. Thus, in addition to grysbok, bushbuck, Cape buffalo, and bushpig, the early Holocene samples dating between roughly 10 000 and 5 000 B.P., are relatively rich in remains of vaalribbok, mountain reedbuck, and roan antelope. In deposits postdating 5 000 B.P., remains of these creatures are much rarer, and the blue duiker, well known in the area historically, makes its first appearance. The precise timing of the faunal shift will probably become clearer as a result of excavations recently completed by R. R. Inskeep in Nelson Bay deposits dating between 5 000 and 3 000 B.P. The implications of the shift are not entirely clear, but broad coincidence with the change in geomorphic processes identified by Butzer at *c.* 4 200 B.P. suggests that it reflects an environmental change, perhaps the establishment of the Knysna Forest in essentially its historic form.

Environmental differences between the earlier and later Holocene are also suggested by differences between the faunal samples from the corresponding levels of Boomplaas Cave A. The faunal differences are at least broadly correlated with differences in the proportions of tree species represented by charcoals (H. J. Deacon 1979). In recent times, the most important source of firewood in the vicinity has been the thorn tree, *Acacia karroo*. It is also the principal tree represented by charcoals in the late Holocene deposits of the site, but it is far less common in the earlier Holocene levels, and it is not represented at all in the late Pleistocene levels, where the principal trees providing charcoal were olive spp. Both olive and thorn trees have dense wood that produces good charcoal, and the change through time almost certainly reflects long-term change in the vegetation rather than changing cultural preferences. Studies of pollens currently under way should shed more light on the nature of the vegetational change and its relationship to contemporaneous faunal changes at Boomplaas.

CONCLUSIONS

Changes in large mammal distributions or species frequencies that probably reflect Upper Pleistocene and Holocene environmental change can be demonstrated to some extent in all the ecozones of southern Africa. However, a pattern of change in mammalian faunas that can be compared to patterns of long-term environmental change established on other grounds can be demonstrated only in the Cape Zone, where cooler intervals repeatedly witnessed an increase in grazing ungulates relative to browsers. In part, the failure to demonstrate comparable patterns in other zones may reflect the fact that Upper Pleistocene environmental and faunal change was greater in the Cape Zone than elsewhere, but in part it almost certainly also reflects the better overall quality of data from the Cape—more well-dated sites and more relatively large faunal assemblages for which detailed numerical data are available. Some authorities believe that it is not really possible to use fossil faunas to document environmental change because it is rarely possible to know the relationship between relative species abundance in a fossil fauna and relative abundance in the live fauna from which the fossils were derived. However, the Cape data show that this is not an insuperable problem, and the contrast between the Cape Zone and others indicates that widespread deficiencies in dating, sample size, and sample description are far more serious obstacles to the palaeoenvironmental interpretation of faunal data.

MAMMALIAN EVIDENCE FOR CULTURAL CHANGE

In archaeological sites, changes in environment and changes in culture are the principal causes of shifts in relative species abundance through time. In situations where the intervals between shifts represent thousands of years, where the shifts are repetitive or cyclical, where they appear to be correlated with changes in environment suggested by other lines of evidence, and where they occur in the absence of evidence for any significant cultural change or innovation, the writer feels it is most economical to ascribe the species fluctuations to environmental change. Most of the fluctuations in large mammal frequencies that can be documented through Upper Pleistocene and Holocene time in southern Africa seem to the writer to occur in circumstances such as the ones that have just been listed, and they have therefore been discussed in the previous section on 'Mammalian Evidence for Environmental Change'. There are, however, some instances of mammalian frequency changes which are not clearly related to environmental change, which are not repetitive or cyclical, and which occur in contexts where there is evidence for major cultural change or innovation.

The most obvious instance of a culturally determined species frequency change is the introduction of domestic stock to southern Africa by Iron Age mixed farmers, beginning about 2 000 years ago (Phillipson 1977). The stock were diffused far beyond the areas ever occupied by Iron Age farmers themselves (H. J. Deacon *et al.* 1978, with references), and some of the late Holocene faunas listed in the last section may be used to establish the route(s) of diffusion (Klein 1979*a*) or the impact the stock may have had on the abundance of some indigenous wild species (Klein 1974*b*). For the open grasslands of the Basutolian region, Maggs (1975) has documented faunal differences that probably reflect major social and technological differences between Iron Age people and broadly contemporaneous Stone Age ones in the same area. The Iron Age faunal samples are richer in large gregarious grazing ungulates, probably because Iron Age peoples could mobilize more manpower for surrounds and drives and could more easily dig game pits that, combined with drives, would constitute the most effective means of obtaining large ungulates in the Basutolian Zone.

The principal concern in this section, however, is not with changes in species frequencies that reflect the introduction of domestic stock or of Iron Age technology and social organization, but rather with a much earlier, more subtle shift in mammal species frequencies that the writer believes may reflect important differences between Middle Stone Age and Later Stone Age peoples in their ability to hunt.

In southern Africa, the term Middle Stone Age (MSA) is currently applied to artefact assemblages dominated by large stone flakes and blades, sometimes altered by retouch into side-scrapers, end-scrapers, points, denticulates, notches, backed pieces, and other tool types conventionally recognized by archaeologists. Handaxes are absent, and microlithic tools are rare. Bone artefacts are also rare, and items of personal adornment or art objects are unknown. Typological and technical variability through space and time is relatively limited, and many differences in typology or flaking technique among MSA assemblages in different regions or at different times may reflect differences in raw material availability more than anything else. The earliest Middle Stone Age assemblages in southern Africa may be as much as 200 000 years old (Butzer, Beaumont & Vogel 1978), while the latest are probably all older than 30 000 years, on the basis of a large series of recently obtained radiocarbon dates (see especially Vogel & Beaumont 1972; Beaumont *et al.* 1978; H. J. Deacon 1979; Klein 1974*a*).

It is presently impossible to characterize the Later Stone Age (LSA) succinctly, in part because the artefact assemblages involved are more variable in time and space than Middle Stone Age ones and in part because only Later Stone Age assemblages post-dating 20 000 B.P. are reasonably well known. LSA assemblages ante-dating 20 000 years have been found at only a handful of sites in southern Africa (Kalemba, Leopard's Hill, Redcliff, Heuningsneskrans, Border Cave, Apollo 11, Elands Bay, and Boomplaas; with references in Tables 2–7), where the samples are either small or remain incompletely described or both. In most LSA assemblages post-dating 20 000 B.P., microlithic tools are a prominent component, but this is not universally true, and, in the Cape Ecozone, there is clear evidence for a 'macrolithic' industry sandwiched between two 'microlithic' ones (J. Deacon 1978). Generally speaking, LSA peoples appear to have produced 'macrolithic' flakes and blades with less care than many MSA peoples. At least the better known LSA assemblages younger than 20 000 B.P. also regularly include standardized bone artefact types (such as 'awls', 'points', 'needles', 'hide-burnishers', and 'fish-gorges'), as well as easily recognizable items of personal adornment or art objects (ostrich egg-shell beads, incised or engraved pieces of ostrich egg-shell or bone, shell pendants, etc.). On the evidence from Border Cave, it seems likely that the manufacture of beads and standardized bone artefacts was practised from the very beginning of the Later Stone Age, more than 30 000 years ago. People making Later Stone Age artefacts of various kinds were still living in much of southern Africa at time of historic contact.

The available evidence suggests strong parallels between the Middle Stone Age and Later Stone Age of southern Africa, as outlined here, and the Middle Palaeolithic (Mousterian) and Upper Palaeolithic of Europe, as they have long been known. Although the Middle Stone Age may have begun somewhat earlier than the Middle Palaeolithic, throughout much of their existence the two were clearly contemporaneous and their terminal dates are very similar. Both exhibit less temporal and spatial variability than the culture-stratigraphic units that succeed them, and both are characterized by the absence of art objects and standardized bone artefact types. One major point of non-comparability may be in the kinds of people associated with them. While the makers of Middle Palaeolithic artefacts were Neanderthals (*Homo sapiens neanderthalensis*), clearly distinct from modern people, the makers of MSA tools may have been anatomically modern (*Homo sapiens sapiens*) (Rightmire 1979), though a pattern of well-documented associations between MSA artefacts and diagnostic human remains will be necessary to show this with reasonable certainty. The makers of Upper Palaeolithic artefacts were certainly anatomically modern, as were at least those Later Stone Age people who lived after 20 000–18 000 B.P.

In Europe, there is substantial evidence to argue that the Upper Palaeolithic represents a quantum advance over what preceded it (Klein 1973), and at least for the moment, the writer feels it is reasonable to hypothesize that the Later Stone Age represents basically the same phenomenon in southern Africa. Under these circumstances, differences between MSA and LSA faunas from sites occupied under broadly similar environmental conditions could be interpreted to reflect cultural evolution. In order to establish such faunal differences, it is of course necessary to have large MSA and LSA faunal samples whose palaeoenvironmental context has been reasonably well established on independent grounds, and these conditions are so far met only in the Cape Ecozone, especially by the Middle Stone Age faunas from Klasies River Mouth and Die Kelders 1 and the Later Stone Age ones from Nelson Bay Cave and Byneskranskop 1.

At all four sites, in levels that were formed when the coast was at or near its present position, bones of seals and penguins are common, but only in the two Later Stone Age sites are they accompanied by large numbers of bones from fish and from flying marine birds. The writer believes this indicates that Later Stone Age people were capable of active fishing and fowling, while Middle Stone Age people were not. With regard to the terrestrial mammal remains that are the principal focus of this paper, there is also an interesting contrast. Comparing layers at Nelson Bay formed during the Holocene to ones that appear to have formed during broadly similar portions of the Last Interglacial at Klasies, the Nelson Bay deposits are significantly richer in remains of pigs and poorer in remains of eland. The LSA levels of Byneskranskop 1 contrast with the MSA ones at Die Kelders in essentially the same way (the comparisons here are restricted to pairs of sites which are located in very similar environments today), though the extent of past environmental comparability is less certain than in the Klasies/Nelson Bay case. In any event, the writer has suggested that the higher frequency of wild pig and lower frequency of eland in the LSA sites reflects the enhanced ability of LSA people to deal with prey that are likely to mount an effective counter-attack on the hunter. Using data on the ages of animals represented in the Nelson Bay and Klasies faunas in addition to the contrasts in relative species frequencies, the writer has further suggested that even when MSA people hunted basically the same species as their LSA successors, they were less effective, that is, they took a smaller proportion of the available animals (Klein 1979*b*).

Clearly, the hypothesis that LSA hunters were more effective than MSA ones would be more secure if it could be demonstrated at additional sites in the Cape Zone and also at sites outside it. The writer has examined the available faunal data from all the other ecozones considered in the previous section of this paper, and only in the Zambesian Zone are there sufficient numerical data for even a preliminary test. Pigs (especially warthog) are more common in both MSA and LSA sites in the Zambesian Zone than in contemporaneous Cape sites, probably reflecting the fact that pigs have always been more abundant in the Zambesian Zone, as they were historically. At the same time, in those Zambesian sites for which numerical data are available, pigs are relatively more frequent in LSA levels (Kalemba, Redcliff, Gwisho, Leopard's Hill, and Makwe) than in MSA ones (Kalemba and Redcliff). However, at Redcliff and Kalemba, where MSA and LSA pig frequencies may be compared within the same sites, the relative increase in pigs is not statistically significant, and it remains possible that the observed differences in pig frequencies between the MSA sites and various LSA ones reflect differences in local environment rather than cultural evolution. Sorting out the alternatives will be possible only with better palaeoenvironmental controls and larger faunal samples. More generally, as in the case of environmental change, the principal obstacle to documenting cultural change from large mammal remains is the shortage of appropriately large, well-described, and well-dated samples.

THE ECOLOGY AND DEMISE OF EXTINCT SPECIES

Not very long ago, it was widely believed that Acheulean cultures had survived into the Upper Pleistocene and that faunas associated with later Acheulean artefacts could even be as recent as 40 000 B.P. The richest such fauna in southern Africa is the one from Elandsfontein (Hopefield) in the southwestern Cape Province (Hendey 1974 with references), which is characterized by at least 19 extinct large mammal species out of approximately 50 that have been identified. The extinct species include a giant gelada baboon (*Theropithecus* (*Simopithecus*) sp.), a sabre-toothed cat (*Megantereon* sp.), an elephant (*Loxodonta atlantica*), a large horse or zebra (*Equus capensis*), two different kinds of pigs (*Mesochoerus* sp. and *Metridiochoerus* sp.), a sivathere (*Sivatherium maurusium*), a small kudu (*Tragelaphus* (*Strepsiceros*) sp.), a giant buffalo (*Pelorovis* sp.), a giant hippotragine antelope (*Hippotragus gigas*), the ancestor (*Rabataceras arambourgi*) of the modern hartebeests, an extinct bastard hartebeest (*Damaliscus niro*), a giant alcelaphine antelope (*Megalotragus* sp.), a large grysbok (*Raphicerus* sp.), a gazelle (*Gazella* sp.), springboks (*Antidorcas recki* and *A. australis*), and some peculiar antelopes whose affinities will perhaps be clarified following E. S. Vrba's current detailed study of the Elandsfontein bovids.

It is now very clear that the Acheulean did not survive into the Upper Pleistocene, and it seems increasingly probable that it was replaced by the Middle Stone Age within the later part of the Middle Pleistocene, more than 130 000 years ago (Klein 1976*b*; Butzer, Beaumont & Vogel 1978; Szabo & Butzer 1979). Furthermore, the overwhelming majority of extinct species represented at Elandsfontein and other Acheulean sites are not represented in Middle Stone Age faunas and in non-archaeological faunas that are contemporaneous with them (see the lists of sites in Tables 2–7 above). Particularly striking in this context is the absence of most of the extinct Elandsfontein species in large earlier Upper Pleistocene faunas in the (same) Cape Ecozone, especially in the very large samples from Klasies River Mouth, where dating of the MSA artefacts and associated fauna to the early Upper Pleistocene is secure. In fact, it appears increasingly likely that most of the extinct species present at Elandsfontein and other Acheulean sites disappeared well before the early Upper Pleistocene, since they are not represented in the large faunal sample from Florisbad, most of which probably comes from a later mid-Pleistocene horizon at the site (Butzer pers. comm.).

The Florisbad fauna contains five extinct species of large mammals—the 'giant Cape horse' (*Equus capensis*), a large warthog (*Metridiochoerus* sp.), a giant buffalo (*Pelorovis antiquus*), a giant alcelaphine (*Megalotragus priscus*), and Bond's springbok (*Antidorcas bondi*). With the addition of the southern springbok (*Antidorcas australis*), these are also the only extinct species which have been found in Upper Pleistocene contexts in southern Africa. Some dentitions assigned to the extant *Damaliscus dorcas* (bontebok/blesbok) in Upper Pleistocene faunas may actually belong to the extinct form *Damaliscus niro*, but horn-cores to prove the presence of *D. niro* are lacking. Additionally, in contrast to Gentry (1978), the writer believes that *D. niro* may be ancestral to Upper Pleistocene and recent *D. dorcas*, in which case it is not extinct in the same sense as the other species considered here. Extinct forms of wildebeest and reedbuck are common in Upper Pleistocene sites in the Cape Ecozone, but were probably just local variants (subspecies) of the black wildebeest and southern reedbuck that survived elsewhere.

The purpose in this section is to present the information that is available on the distribution and ecology of the extinct species followed by a brief consideration of the causes of extinction. Teeth of the various extinct forms are illustrated in Figures 3–5.

EQUUS CAPENSIS

The writer has followed Churcher & Richardson (1978; also Churcher 1970) in assigning all large later Pleistocene horses in southern African sites to the species *Equus capensis* (including '*E. helmei*', '*E. plicatus*', *et al.*) Upper Pleistocene specimens assignable to *Equus capensis* have been found in all six ecozones

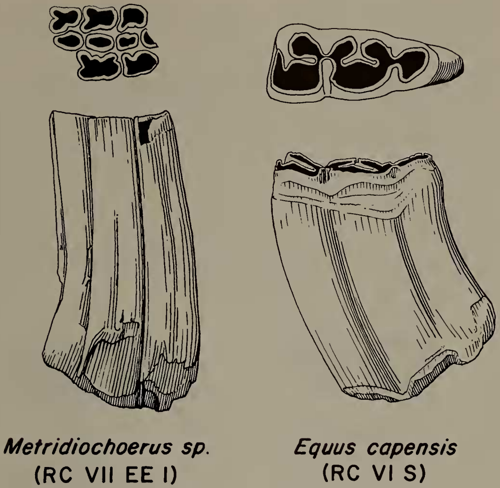


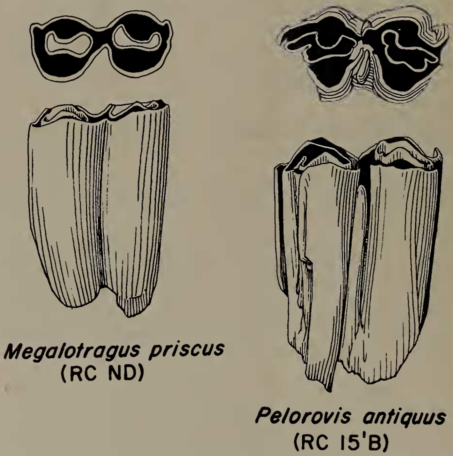
Fig. 3. A fragmentary third molar of *Metridiochoerus* sp. and a lower third molar of *Equus capensis*. Both specimens come from Redcliff Cave, Zimbabwe Rhodesia, and are reproduced natural size. (Drawings by K. Scott.)

considered earlier: at Redcliff in the Zambesian Zone; at Pomongwe, Chelmer, Kalkbank, the Cave of Hearths, Bushman Rock Shelter, Border Cave, and Aloes in the Transvaalian Zone; at Equus Cave, Black Earth Cave, and ≠gi in the Kalaharian Zone; at Florisbad, Vlakkraal, and Koffiefontein in the Basutolian Zone; at Apollo 11 and Elands Bay Caves in the Karoo–Namaqualian Zone; and at Sea Harvest, Hoedjies Punt, Swartklip, Bloembos, Duinefontein, Byneskranskop 1, and Boomplaas in the Cape Zone.

On the evidence from Apollo 11, Elands Bay, Byneskranskop 1, and Boomplaas, *Equus capensis* probably made its last appearance in the Karoo–Namaqualian and Cape Zones between 12 000 and 10 000 years ago. In the Zambesian Zone, it is known from the 'Tshangula' horizons at Redcliff, where it may be as young as 20 000 B.P. In other zones, it cannot be shown to have survived 40 000–30 000 B.P., but this probably reflects the very small number and small size of faunal samples that date between 40 000–30 000 and 10 000 B.P.

in these zones. In essence, the time when *E. capensis* made its last appearance outside the Karoo–Namaqualian and Cape Zones remains to be established.

In most Upper Pleistocene sites in southern Africa and in all those which have provided large samples, *Equus capensis* is accompanied by one or more of its smaller, historic relatives—Burchell's zebra, quagga, or mountain zebra. In most sites, it is much less common than the smaller form(s), but in Karoo–Namaqualian sites, located in what is and perhaps always has been the driest of the southern African ecozones, and in sites in the drier, western portion of the Cape Ecozone, it is relatively more common (versus smaller equids). Additionally, in the Zambesian Zone, at Redcliff, where *E. capensis* is not particularly frequent overall, it is most frequent in the 'later Bambata' horizons, which sedimentological evidence suggests were formed under comparatively arid conditions. The possibility that *E. capensis* preferred or was relatively well adapted to arid environments is especially interesting, since some authorities believe it was ancestral to the living Grevy's zebra of northern Kenya, southern Ethiopia, and Somalia (Churcher & Richardson 1978). Among the living zebras,


Megalotragus priscus
(RC ND)

Pelorovis antiquus
(RC 15'B)

Fig. 4. Lower molars of *Megalotragus priscus* and *Pelorovis antiquus*. Both specimens come from Redcliff Cave, Zimbabwe Rhodesia, and are reproduced natural size. (Drawings by K. Scott.)

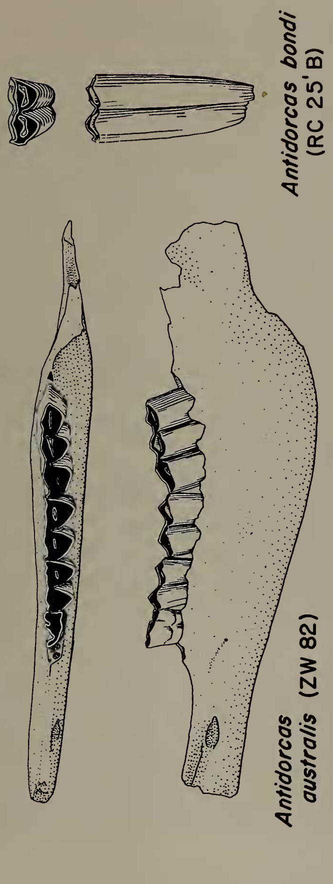


Fig. 5. A mandible of *Antidorcas australis* from Swartklip 1, south-western Cape Province, South Africa, and a lower molar of *Antidorcas bondi* from Redcliff Cave, Zimbabwe Rhodesia. Both specimens are reproduced natural size. (Drawings by K. Scott.)

Grevy's appears to be the least dependent upon water. It inhabits some of the most arid country in east Africa, overlapping Burchell's zebra on the margins of its range, but occurring alone in the arid core.

METRIDIOCHOERUS SP.

The writer has followed White and Harris (1977) in assigning all large warthog-like pigs of the later Pleistocene to the genus *Metridiochoerus* (including '*Stylochoerus*', '*Tapinochoerus*', *et al.*), though not all specialists agree with their taxonomy (Cooke 1978). In any case, the large pigs involved are so far very rare in Upper Pleistocene contexts, having been recorded only at Koffiefontein, Vlakkraal, and Florisbad in the Basutolian Ecozone (the Florisbad specimens may be largely or wholly of mid-Pleistocene age), and at Redcliff Cave in the Zambesian Zone. Among these occurrences, the latest is perhaps at Redcliff, where a large warthog-like pig is still present in the 'Tshangula' horizons, tentatively dated to between 30 000 and 20 000 B.P. in discussion above.

Estimates of *Metridiochoerus* abundance are available only from Redcliff where the creature is very rare, too rare to search for frequency covariation with extant species that might indicate shared habitat preferences. Its highly hypsodont molars, similar in structure to those of the warthog, plainly indicate it was a grazer, which is in keeping with the predominance of grazers at Redcliff and in the Basutolian faunas in which *Metridiochoerus* has been identified.

PELOROVIS ANTIQUUS

The writer has followed Gentry (1978) in assigning all the 'giant', long-horned Upper Pleistocene buffaloes of southern Africa to this species (including especially material formerly assigned to '*Homoioceras baini*'). Fossils of *Pelorovis antiquus* have been found at Redcliff in the Zambesian Zone; at Kalkbank and the Cave of Hearths in the Transvaalian Zone; at ≠gi in the Kalaharian Zone; at Florisbad, Vlakkraal, Koffiefontein, and Driefontein in the Basutolian Zone; at Elands Bay Cave in the Karoo–Namaqualian Zone; and at Sea Harvest, Hoedjies Punt, Ysterfontein, Bloembos, Swartklip, Die Kelders, Nelson Bay, Boomplaas, and Klasies River Mouth in the Cape Zone. The species was thus very widespread, but it is generally not common in fossil faunas, except in the Basutolian Zone, where it has also been recorded as an apparently isolated fossil at various localities, for example, in the alluvium of the Modder River, which provided the first giant buffalo fossil to be scientifically recorded in southern Africa (Cooke 1955).

Finds at Nelson Bay and Elands Bay Caves suggest *P. antiquus* made its last appearance in the Cape and adjacent parts of the Karoo–Namaqualian Zone between 12 000 and 10 000 years ago. Elsewhere, it cannot be shown to have survived beyond 40 000–30 000 B.P., but, as in the case of *Equus capensis*, this probably reflects the absence of large faunal samples from the interval between 40 000–30 000 and 10 000 B.P. The date of its last appearance outside the Cape and Karoo–Namaqualian Zones thus remains to be established.

The hypsodont teeth and exceptionally long horns of *P. antiquus* (spanning

2–3 m) both point to a preference for relatively open, grassy environments, also perhaps suggested by the relative abundance of the species in Basutolian sites. It seems likely that *P. antiquus* was more at home in open settings than its closest living relative, the Cape buffalo. Ecological distinction from the Cape buffalo is implied at Klasies River Mouth, where the frequencies of the two species vary independently of one another from level to level within the deposits. At Klasies, the frequency of giant buffalo is correlated most closely with that of eland, which may suggest a common environmental preference. Eland, as studied by Hillman (1974), appear to favour open country with large islands and galleries of tree and shrub growth. The Basutolian sites at which giant buffalo are common are all located near streams or springs where such islands or galleries probably occurred. The giant buffalo may have gravitated to them for shade rather than for food.

At Klasies, there are enough giant buffalo dentitions for an analysis of the ages at which individual animals died or were killed by the Middle Stone Age occupants of the site (Klein 1978*d*, 1979*b*). Most of the individuals present were within the first 10 per cent of potential lifespan (many were newborn), while among older animals, prime adults (between 20% and 50% of lifespan) were especially rare. The Klasies giant buffalo age distribution is very similar to the natural (attritional) mortality pattern in all free-ranging large ungulates, to the age distribution in recently observed Cape buffalo killed by lions, and to the age distribution of Cape buffalo in the same Klasies MSA levels. Recent observations indicate that it is large size and membership in large herds that make Cape buffalo prime adults largely immune to lion predation. The age distribution of Cape buffalo at Klasies suggests that the MSA occupants were constrained by the same features as lions in dealing with Cape buffalo, and the similarity between the Cape buffalo and giant buffalo distributions suggests that large size and herd membership may also be the reasons that giant buffalo prime adults are rare at Klasies. Given the resemblances between the giant buffalo age profile at Klasies and the probable natural (attritional) mortality pattern in giant buffalo, it is even conceivable that the Klasies people did not prey on giant buffalo at all, but scavenged individuals which had died naturally or been killed by other predators.

MEGALOTRAGUS PRISCUS

The writer has followed Gentry (1978) in assigning all the later Pleistocene 'giant alcelaphines' of southern Africa to the single species *Megalotragus priscus* (including '*Pelerocerus*' spp, '*Lunatoceras mirum*', '*Alcelaphus helmei*', *et al.*). Upper Pleistocene fossils of *M. priscus* have been found at Leopard's Hill and Redcliff in the Zambesian Zone; at Chelmer and Kalkbank in the Transvaalian Zone; at Equus Cave, Black Earth Cave, Gobabis, and ≠gi in the Kalaharian Zone; at Florisbad, Vlakkraal, Koffiefontein, and Driefontein in the Basutolian Zone; and at Hoedjies Punt, Boomplaas, and Nelson Bay Cave in the Cape Zone. Outside the Basutolian Zone, *M. priscus* is generally not a common element in fossil faunas; within this zone, it is not only well represented at the sites listed above but has been found as an isolated fossil or with presently unclear associations at a variety of other sites, including especially the alluvium of the Modder River, which provided the holotype specimen.

Its hypsodont teeth, the dietary preferences of all its closest living relatives (hartebeests, wildebeests, and bastard hartebeests), its former distribution, and its clear tendency to be most common in fossil faunas heavily dominated by grazers, indicate beyond all doubt that *M. priscus* was a grazer. Its latest known occurrence is in deposits at Nelson Bay Cave radiocarbon-dated to approximately 16 000 B.P., but it is a rare element in the Nelson Bay fauna, and the possibility is good that it persisted, like *Equus capensis* and *Pelorovis antiquus*, in the Cape Zone somewhat later, perhaps to between 12 000 and 10 000 B.P. At Leopard's Hill in the Zambesian Zone, its provenience within the site is uncertain, but it is almost certainly younger than 24 000 radiocarbon years (the approximate age of the oldest fossiliferous deposits at the site). Elsewhere, it cannot be shown to have survived beyond 40 000–30 000 B.P., but again, as in the case of *Equus capensis* and *Pelorovis antiquus*, this may well reflect the rarity of large faunal samples from the interval 40 000–30 000 to 10 000 B.P., rather than the absence of the species.

ANTIDORCAS BONDI

Cooke and Wells (1951) initially described this hyperhypsodont antilopine antelope as *Gazella bondi*. However, Vrba (1973) has demonstrated that the frontals of this species were inflated below the horn-cores, a feature that is characteristic of *Antidorcas* and not of *Gazella*. For this and other reasons, the species is better placed in *Antidorcas* (Gentry 1978).

Upper Pleistocene fossils of *A. bondi* are known from Redcliff in the Zambesian Zone; from Chelmer, the Cave of Hearths, and Border Cave in the Transvaalian Zone; from Gobabis, Witkrans, Equus Cave, and Black Earth Cave in the Kalaharian Zone; and from Florisbad, Vlakkraal, and Driefontein in the Basutolian Zone. Its absence so far in the Karoo–Namaqualian Zone may be a result of inadequate sampling, but its failure to occur in Cape faunas may reflect true absence, since the Cape samples in which it might be expected are relatively large.

The latest record of *A. bondi* is at Border Cave in a level radiocarbon-dated to approximately 38 000 B.P. However, the date of its last appearance remains unestablished, since large samples dating to between 38 000 and 10 000 B.P. are unknown in those ecozones where the species was most common.

Its hyperhypsodonty, geographic distribution, and the species with which it occurs all indicate clearly that *A. bondi* was primarily a grazer. This is shown particularly well at Border Cave, where there is alternation between levels dominated by grassland species and ones dominated by species that prefer bushier settings. *A. bondi* is plainly most common in those levels where grassland animals are most abundant.

ANTIDORCAS AUSTRALIS

Hendey and Hendey (1968) originally described this species as a subspecies of the common springbok, *Antidorcas marsupialis*. However, Hendey (1974) concluded it was more likely to be a separate species, since, at the mid-Pleistocene locality of Elandsfontein, it was apparently sympatric with *A. recki*, the probable ancestor of the common springbok. Upper Pleistocene fossils of *A. australis* have been found only in the Cape Ecozone where it was widespread. Its last recorded occurrence is in deposits at Nelson Bay Cave dated to between 12 000 and 10 000 B.P.

A. australis had horn-cores that were more mediolaterally compressed than those of *A. marsupialis* and that did not bend sharply backwards and outwards. It was also somewhat smaller on average than *A. marsupialis*, but in most other important respects, including the morphology of the dentition, it was very similar to *A. marsupialis*. *A. marsupialis* is not known to have occurred in the Cape Zone in Upper Pleistocene (or recent) times, except on the peripheries, and it seems likely that *A. australis* filled the niche for a small selective grazer also capable of some browsing that *A. marsupialis* filled and still fills in neighbouring ecozones. Like the frequency of *A. marsupialis*, that of *A. australis* in fossil sites is closely linked to the frequency of 'plains' species, such as wildebeest, bastard hartebeest, and zebra.

THE CAUSES OF EXTINCTION

As in other parts of the world, the causes of late Pleistocene mammalian extinctions in southern Africa are a subject of considerable interest, particularly given the very real possibility that early people were involved. The other major 'cause' which has been postulated is environmental change.

The writer believes that environmental change played a role in late Pleistocene extinctions, but it can nowhere be the sole reason, since the species that became extinct repeatedly survived the same kinds of environmental change earlier on in the Pleistocene. This can be shown especially clearly in the Cape Ecozone where the extinction of the giant Cape horse, giant buffalo, southern springbok, local subspecies of the black wildebeest and southern reedbuck, and probably also the giant alcelaphine occurred roughly 12 000–10 000 years ago, at a time when it is clear that fynbos, bush, and forest were replacing much of the grassland that had existed previously. The species that disappeared were all primarily grazers, which probably did suffer a shrinkage in both numbers and range as a result of the vegetational change. However, the same kind of vegetational change characterized similar climatic shifts earlier on in the Cape Zone (that is, earlier transitions from 'glacial' to 'interglacial' conditions). During these earlier shifts, at least some of the extinct species appear to have become less numerous, but they all survived.

Environmental change is thus not a sufficient explanation for extinctions in the Cape Zone, and the principal factor which differentiated the period of extinction, 12 000–10 000 years ago, from earlier periods of comparable environmental change was perhaps the presence of more proficient hunters, as discussed in the previous section of this paper. The writer believes that it is entirely possible that Stone Age people in the Cape, faced with a decline in the 'plains' game on which they had depended for generations, intensified their pursuit of those that were left, perhaps through technological innovation driving the numbers of some species below a critical threshold and impairing their reproductive capacity. Extinction would follow, even if people were not responsible for killing the very last animal.

Outside the Cape Ecozone, the hypothesis that people were responsible for late Pleistocene extinctions is much more tenuous. It seems likely that the extinctions occurred after Later Stone Age peoples had replaced Middle Stone Age ones in other ecozones, but evidence that these Later Stone Age peoples were more proficient hunters is so far lacking. Additionally, the timing of extinctions outside the Cape Zone remains unclear, mainly because there are no large faunal assemblages elsewhere dating from the critical period between 40 000–30 000 and 10 000 B.P. Finally, even if it is assumed that the extinctions outside the Cape Zone took place 12 000–10 000 B.P., as they did inside it, the nature of environmental change in this interval is not as well established as in the Cape, and it is far from certain that it would have adversely affected the extinct species in the way it probably did in the Cape. This is important, because the hypothesis offered above requires an environmental stimulus for any human role in extinction.

Clearly, further elucidation of the causes of late Pleistocene extinctions in southern Africa will require the recovery of large late Pleistocene faunal samples from various ecozones. These are necessary not only for more precise estimates of the timing of extinctions and of the nature of any environmental change that may have accompanied them, but also for determining if the extinct species experienced long periods of decline or if they disappeared rather abruptly, as appears to be the case in the Cape Zone. Additionally, large samples may allow the construction of age/sex profiles to determine if the extinct species underwent demographic changes through time that might indicate impaired reproductive capacity or changing patterns of human predation. In sum, as in the case of demonstrating environmental and cultural change from faunal remains, elucidating the causes of extinction is not so much a theoretical problem as it is a practical one of obtaining large, well-excavated, and well-described faunal assemblages from contexts where good data on artefacts, sediments, pollen, and so forth provide controls for comparisons designed to separate the cultural and environmental variables responsible for assemblage composition.

CONCLUSIONS

In the overwhelming majority of cases, it is impossible to assume a one-to-one relationship between the relative abundance of species in a fossil mammal assemblage and their relative abundance in the live community from which they were drawn. Almost always, it is far safer to assume that the agency of accumulation has altered the original frequency relationships, and it is usually impossible to say how much. Thus, for example, the fact that a particular archaeological faunal assemblage consists three-quarters of grazers and one-quarter of browsers does not mean that the grazer/browser ratio in the ancient environment was 3 : 1 or even that grazers were more numerous than browsers. It may be that the people responsible for the bones found it easier to obtain grazers, or that grazers, since they are often larger, provided a higher return for time and effort in the hunt. Whatever the case, the extent to which the people may have altered or 'biased' the original grazer/browser ratio is probably unknowable.

Superficially then, detailed interpretation of fossil mammal assemblages may appear impossible from the outset. However, this is only the case if the goal is to make precise statements about the live abundance of various species or about the subsistence behaviour of people at single instants in past time. It is not true if the focus is on *changes* in live abundance or in cultural practices through time, since, in this case, it is possible to introduce controls for the effects of environment or culture. As an example, take two faunas of different ages from neighbouring archaeological sites or from different levels within the same site. If there is evidence from pollen, sediments, oxygen-isotope ratios in associated marine shells, etc., that the faunas were accumulated under very similar environmental circumstances, it seems reasonable to suppose that any differences in species frequencies between them reflect differences in human behaviour.

Similarly, if there is sound associated evidence for differences in past environment and no artefactual evidence for significant differences in culture, then it is probably most reasonable to conclude that any differences in species frequencies between faunas reflect differences in past environments. As a more concrete example, take two faunas from successive levels in the same site containing broadly similar artefacts, but in sedimentary contexts suggesting important differences in palaeoenvironment. If the fauna of one level contains relatively more grazers than the fauna of the other, it seems most reasonable to conclude that grazers were more common on the hoof at the time the first level formed, even though the live abundance of grazers in the ancient environment of either level remains unknown or unknowable.

Basically then, faunal samples are far more useful for establishing *changes* in environment or culture through time than for reconstructing environments or cultural practices at particular points in time. However, it is obvious that changes may be determined only through comparisons among samples, with controls provided by accompanying pollen, sediments, artefacts, and so forth, as well as by detailed characteristics of the bone assemblages themselves. From this, it follows, first, that faunal analysis is inextricably dependent upon other fields—conventional archaeology, palynology, sedimentology, isotope geo-chemistry, etc.—if interpretations are to be secure. Second, it is obvious that no single sample is ever likely to be very informative. Rather, it is necessary to have many samples to permit as wide a range of controlled comparisons as possible. It is, of course, also important that the samples be large, well described, and well excavated, to enhance the chances that significant patterns will emerge in the process of comparison.

Among the six southern African ecozones considered in this paper, only the Cape Zone has provided a sufficient number of large, well-described, and well-excavated faunal samples, accompanied by sufficient contextual information, to isolate patterns of mammalian frequency change that probably reflect systematic changes in environment and culture during the Upper Pleistocene and Holocene. The Cape data suggest (i) that Upper Pleistocene intervals of cooler climate locally witnessed the expansion of grass at the expense of fynbos, bush, and forest; (ii) that local Middle Stone Age peoples, living prior to 40 000–30 000 B.P., were less proficient hunter–gatherers than their Later Stone Age successors; and (iii) that a combination of environmental change and the greater hunting proficiency of Later Stone Age peoples was responsible for the extinction of several large mammal species in the Cape Zone 12 000–10 000 B.P. The last two hypotheses are clearly of broad anthropological or evolutionary interest and certainly deserve investigation in other ecozones, as well as further testing in the Cape Zone. Ultimate demonstration of the likelihood that they are correct is not basically a theoretical problem, but a practical one of obtaining numerous large faunal samples from carefully documented contexts.

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APPENDIX

VERNACULAR AND SCIENTIFIC NAMES OF THE EXTANT MAMMALIAN SPECIES MENTIONED IN THE TEXT

VERNACULAR NAME	SCIENTIFIC NAME
hedgehog	*Erinaceus frontalis*
Cape hare	*Lepus capensis*
scrub hare	*Lepus saxatilis*
red rock hare	*Pronolagus crassicaudatus*
springhare	*Pedetes capensis*
cane rat	*Thryonomys swinderianus*
porcupine	*Hystrix africae-australis*
Cape mole-rat	*Bathyergus suillus*
chacma baboon	*Papio ursinus*
yellow baboon	*Papio cynocephalus*
vervet monkey	*Cercopithecus aethiops*
side-striped jackal	*Canis adustus*
black-backed jackal	*Canis mesomelas*
Cape hunting dog	*Lycaon pictus*
spotted hyena	*Crocuta crocuta*
brown hyena	*Hyaena brunnea*
lion	*Panthera leo*
leopard	*Panthera pardus*
cheetah	*Acinonyx jubatus*
Cape fur seal	*Arctocephalus pusillus*
gazelle seal	*Arctocephalus gazella*
elephant seal	*Mirounga leonina*
crab-eater seal	*Lobodon carcinophagus*
rock hyrax	*Procavia capensis*
tree hyrax	*Dendrohyrax arboreus*
elephant	*Loxodonta africana*
Grevy's zebra	*Equus grevyi*
Burchell's zebra	*Equus burchelli*
quagga	*Equus quagga*
mountain zebra	*Equus zebra*
black rhinoceros	*Diceros bicornis*
white rhinoceros	*Ceratotherium simum*
hippopotamus	*Hippopotamus amphibius*
warthog	*Phacochoerus aethiopicus*
bushpig	*Potamochoerus porcus*
giraffe	*Giraffa camelopardalis*
okapi	*Okapia johnstoni*
eland	*Taurotragus oryx*

VERNACULAR NAME	SCIENTIFIC NAME
bongo	*Boocercus euryceros*
greater kudu	*Tragelaphus strepsiceros*
nyala	*Tragelaphus angasi*
sitatunga	*Tragelaphus spekei*
bushbuck	*Tragelaphus scriptus*
gemsbok	*Oryx gazella*
roan antelope	*Hippotragus equinus*
sable antelope	*Hippotragus niger*
waterbuck	*Kobus ellipsiprymnus*
puku	*Kobus vardoni*
lechwe	*Kobus leche*
southern reedbuck	*Redunca arundinum*
mountain reedbuck	*Redunca fulvorufula*
Cape (= red) hartebeest	*Alcelaphus buselaphus*
Lichtenstein's hartebeest	*Alcelaphus lichtensteini*
tsessebe	*Damaliscus lunatus*
bontebok and blesbok	*Damaliscus dorcas*
bastard hartebeest	*Damaliscus* spp.
blue wildebeest	*Connochaetes taurinus*
black wildebeest	*Connochaetes gnou*
impala	*Aepyceros melampus*
Grant's gazelle	*Gazella granti*
Thomson's gazelle	*Gazella thomsoni*
springbok	*Antidorcas marsupialis*
blue duiker	*Cephalophus monticola*
common (= grey) duiker	*Sylvicapra grimmia*
oribi	*Ourebia ourebi*
klipspringer	*Oreotragus oreotragus*
steenbok	*Raphicerus campestris*
Sharpe's grysbok	*Raphicerus sharpei*
Cape grysbok	*Raphicerus melanotis*
vaalribbok	*Pelea capreolus*
domestic sheep	*Ovis aries*
domestic goat	*Capra hircus*
Cape buffalo	*Syncerus caffer*
domestic cattle	*Bos taurus*